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Ecological patterns during ontogeny in the bicolor damselfish, Stegastes partitus, Poey

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ECOLOGICAL PATTERNS DURING ONTOGENY IN THE BICOLOR DAMSELFISH, *STEGASTES PARTITUS*, POEY

BY

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ABSTRACT

ECOLOGICAL PATTERNS DURING ONTOGENY IN THE BICOLOR DAMSELFISH, *STEGASTES PARTITUS*, POEY

by

Richard Stephen Nemeth

University of New Hampshire, September, 1996

This dissertation examined the ecological constraints during the early life history of the bicolor damselfish, *Stegastes partitus* Poey (Perciformes, Pomacentridae). A series of studies, conducted in Teague Bay, St. Croix and Discovery Bay, Jamaica between 1991 and 1996, determined the cause of variation in length of the planktonic larval period, the effect of larval history on settlement success and examined the causes behind the patterns of distribution and population structure seen throughout its geographic range. Variable growth rates in early-stage larvae established a canalized trajectory toward larval competence and provides a mechanism for determining planktonic duration. Using otolith microstructure I determined that larvae with the fastest growth rates during the first 10 days post-hatching had planktonic durations up to 15 days shorter than larvae with the slowest growth rates. Moreover, there was a positive correlation between pre- and post-settlement growth. With a series of experiments, I determined that larval settlement behavior of *S. partitus* was most important in determining small-scale (10's of meters) distribution patterns and that differential survival after settlement enhanced these initial patterns. Survival was related to the

structural architecture of different substrates which determined refuge suitability and predation risk. During ontogeny, juvenile bicolor damselfish can increase their overall fitness by selecting small rubble substrates at settlement then switching to adult substrates at maturity. Juveniles selecting this strategy had a 50% increase in survivorship over larvae which settled directly to the adult coral substrate. I interpret these results with a graphical model and discuss its relevance to identifying trade-offs and predicting habitat shifts during ontogeny. At larger spatial scales (100's of meters) larval recruitment was of minor importance in structuring adult populations in St. Croix. The additive effects of interspecific competition, food supply, and the physical and biological features of various reef habitats significantly affected juvenile growth. A prolonged juvenile period, due to reduced growth, indirectly affected mortality and thus adult abundance. These effects were nearly identical on St. Croix and Jamaican barrier reefs and were altered only by site-specific predation intensity. The relative importance of these various ecological constraints on life history patterns is discussed.

CHAPTER I

EFFECTS OF VARIATION IN LARVAL GROWTH AND SETTLEMENT BEHAVIOR ON THE EARLY LIFE HISTORY OF THE CARIBBEAN DAMSELFISH, *STEGASTES PARTITUS* POEY

SUMMARY

Complex life cycles are adaptations that exploit transient opportunities for growth and dispersal in different habitats during different ontogenetic stages. The passage from the pelagic to benthic environment, undertaken by most marine organisms, is a crucial transition where processes experienced as larvae and decisions made at settlement may determine an individual's success. This study examined the ecological constraints on several stages in the early life history of the bicolor damselfish (*Stegastes partitus*, Poey) and their relative cumulative effects on its abundance and population structure. A series of experiments, conducted in Teague Bay, St. Croix, U. S. V. I., determined the effect of larval history (e.g. growth rate and planktonic duration) on settlement success, whether post-settlement distribution patterns were determined by larval behavior or differential survival and whether juvenile and adult abundance were determined by recruitment or benthic processes.

By analyzing otolith increment widths I found that larval growth rates in early-stage larvae established a canalized trajectory toward larval competence and provides a mechanism for determining variation in planktonic duration. Larvae with fast (9.89 μm/d), average (8.96 μm/d) and slow (7.77 μm/d) otolith growth rates during the first 10 d post-hatching had short (mean=20 d, 18-21 d), average (mean=24 d, 22-26 d) and long (mean=28 d, 27-33 d) larval durations. Moreover, late pelagic (larval) and early benthic (juvenile) growth rates were positively correlated whereas size and age at settlement had no effect on postsettlement survivorship or growth. Other experiments revealed that within the fore reef zone larval settlement behavior was most important in determining small-scale (10's of meters) distribution patterns of *S. partitus*. Differential survival after settlement enhanced these initial patterns. Depending on reef zone (back reef vs. fore reef), the abundance of *S. partitus* adults was influenced to varying degrees by both juvenile demography and recruitment. In the fore reef, growth and survival of juvenile *S. partitus* were two-fold greater than for fish living in the back reef. Slower growth and greater mortality on the back reef were attributed to greater levels of interspecific competition with other territorial pomacentrids and to differences in physical and biological features of the reef which affected food supply. Mortality rates of *S. partitus* in the back reef of Teague Bay produced a greater change in adult population density than did variation in recruitment.

INTRODUCTION

Complex life cycles incorporate changes in an organism's physiology, morphology and behavior as it passes from one ontogenetic stage to another. These ontogenetic changes exploit transient opportunities for growth and dispersal in different habitats (Wilbur 1980). The larval stages of insects and anurans, for example, are relatively sedentary and specialized for growth whereas the adult stages are specialized for dispersal (Johnson 1966; Wilbur 1974). In contrast, benthic marine invertebrates and fishes have planktonic larvae specialized for dispersal while sedentary juveniles and adults maximize growth (Thorson 1950; Ehrlich 1975; Sale 1980; Sinclair 1988). The dispersive larval stage of sessile and sedentary marine organisms functions as a means of colonizing patchily distributed habitats or unpredictable environments while spreading the risk of local extinction across a wide geographical range (Barlow 1981; Doherty et al. 1985). During the pelagic stage, which lasts from days to months (Victor 1986; Wellington and Victor 1989), marine fish larvae will encounter an array of biological and physical conditions that influence their rate of development, larval duration and survival (Thorson 1950; Hunter 1981; Thorrold et al. 1994). Sources of variation in larval history and the influence of larval history on post-settlement events, however, are still largely unknown (but see Bertram and Leggett 1994).

When a larva makes the transition to the reef environment, its fitness will be maximized if it selects a place to live where predation is minimized and growth is maximized (Gilliam and Fraser 1987). Evidence indicates that pelagic larvae can "test" the substratum prior to settlement (Marliave 1977;

Sale et al. 1980; Marliave 1986) often rejecting a site and returning to the plankton (Connell 1961; Raimondi 1990; Kaufman et al. 1992). These larvae may be responding to single or multiple cues ranging from habitat and microhabitat characteristics (Sale et al. 1984; Breitburg 1989, 1991; Levin 1991; Booth 1992; Wellington 1992) to the presence of conspecifics and other species (Shulman et al. 1983; Sweatman 1985a). While patterns in post-larval distribution, growth and mortality have been detected in a number of reef fish species (Doherty 1981; Jones 1986, 1988; Wellington 1992), the habitat characteristics responsible for these patterns and their relative importance to subsequent juvenile and adult demography remain unknown (Hadfield 1986; Richards and Lindeman 1987; Jones 1991).

This paper addresses two primary questions: 1) Can larval history (larval growth and planktonic duration) be used to predict post-settlement events?, and 2) Do post-settlement processes reinforce or alter patterns of larval settlement among various substrates (scale of meters) and among different habitats (scale of 100's of meters)? Tropical coral reefs are ideal environments in which to test these hypotheses because most coral reef fishes (e.g. Pomacentridae) are strongly site attached and the habitats into which they settle vary in their physical and biological parameters. Habitat characteristics such as the structure of the substrate, the abundance of resources and the number and types of competitors and predators may affect fish populations in predictable ways (Jones 1991). Larval preference for different reef zones or different substrates may create conspicuous patterns of abundance. Differential mortality and growth of juveniles will enhance or alter these initial patterns established at settlement. For more sedentary species, the cumulative effects of these early life history events will have a greater influence on the abundance and distribution of their adults.

This study examined the relative cumulative effects of larval history and larval preferences at settlement on the small-scale (among substrates) distribution patterns of bicolor damselfish (*Stegastes partitus*, Poey) juveniles. Larval duration and larval growth were determined from the information preserved in fish otolith microstructure whereas a natural settlement experiment determined larval preferences for different substrates and for the presence of conspecific adults. A second experiment documented variations in behavioral interactions and demographic rates of juveniles among reef habitats which provided evidence for the processes responsible for the distinct size-class distribution of bicolor damselfish among reef habitats.

MATERIALS AND METHODS

Study Site

Sampling and experiments were conducted in Teague Bay, St. Croix, United States Virgin Islands. Teague Bay is enclosed by a bank-barrier reef on the northeast coast of St. Croix. The tidal exposed reef crest separates the shallow back reef lagoon (5 - 8 m deep) from the fore reef slope and fore reef base (10 - 15 m). The shallow back reef (1 - 5 m) and shallow fore reef slope (1 - 10 m) are composed primarily of dead *Acropora palmata*, large live and dead *Porites porites* colonies, massive *Montastrea annularis* coral heads and a variety of other head coral species. The back reef slope varies in width from 2 to 10 m and gives way to sand substrate. Within the lagoon isolated patch reefs composed of live *M. annularis* colonies or dead colonies covered with

macroalgae are scattered throughout. Between patch reefs are beds of *Thalassia testudinum* or large areas of fine sandy sediments abundant with the conical mounds of *Arenicola cristata* lugworms. The fore reef slope (10 to 50 m wide) descends to the reef base where isolated coral heads and patch reefs are surrounded by sand. Massive heads of *M. annularis* dominate the fore reef base along with sea fans, gorgonians and sponges. Fifty to 100 m seaward from the reef slope are expansive manatee grass (*Syringodium filiforme*) beds.

Several terms used frequently are defined here for clarity. Habitat is an area within a physiographic zone (fore reef, back reef) composed of a mosaic of different substrate types. For example, *A. palmata, M. annularis* and *P. porites* corals (substrates) thrive on reef base or reef slope habitats within the fore reef zone. Examples of other substrate types within a habitat include sponges, dead coral rubble (e.g. *P. porites* and *A. cervicornis*), sea grass (e.g. *Thalassia testudinum*) and sand. Microhabitats are specific locations within a substrate type. For example, the base and top of a massive *M. annularis* coral head are considered as two distinct microhabitats within this substrate.

Study Species

The bicolor damselfish *Stegastes partitus*, Poey (Perciformes, Pomacentridae) is abundant and ubiquitous in the Caribbean (Emery 1968). Its larvae emerge from demersal eggs in 4-6 days at 2.1 mm length and settle from the plankton between 18 to 45 days at 10.4-15 mm (Robertson et al. 1988, 1990; Wellington and Victor 1989). Larvae apparently remain pelagic throughout their larval life although Emery (1968) found some pre-competent larvae buried in the sand of the deep fore reef at night. Settlement

typically occurs during a 5 to 13 day period around the new moon creating a uni-modal cycle (Robertson et al. 1988, 1990).

Newly settled recruits and small juveniles (10-25 mm SL) are most abundant in shallow (<10 m) back reef and fore reef locations (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980; pers. obs.). Recruits typically occupy rubble patches (*Porites porites, P. furcata, Acropora cervicornis, A. palmata*) in the sand or small, low patch reefs of living coral (Emery 1968; pers. obs.). Adults and large juveniles (>30mm SL) are most abundant in fore reef locations (10 to 30 m) living on boulder corals such as *Montastrea annularis* and on large sponges (Emery 1968). *S. partitus* reaches sexual maturity within a year (Schmale 1981).

A gradual dietary shift from benthic algae and invertebrates to planktonic algae and invertebrates occurs with increasing size (Emery 1968). (Emery 1968, 1973) found that the diet (measured in percent volume of items) of juveniles and young adults (10-50 mm SL) was mainly comprised of benthic algae (62-75 %), copepods (6-20 %) and filamentous pelagic algae (*Trichodesmium thiebaulti*, 5-23 %). Adult diet composition in order of importance was filamentous pelagic algae (48-80 %), benthic algae (17-38 %), pelagic tunicates (*Oikopleura*, 6-7 %) and other items.

Settlement and Recruitment Experiments

Larval settlement patterns and subsequent mortality were examined between 29 July and 24 August, 1992 and between 15 June and 20 August, 1994 on the fore reef base of Teague Bay. Two nearby sites, east fore reef (EFR) and west fore reef (WFR), approximately 100 m apart and 15 m deep were selected based on availability of isolated *Montastrea annularis* coral heads and dead

coral rubble. These two substrates are commonly occupied by bicolor damselfish. At each site, I selected twelve *M. annularis* coral heads, measured their circumference (C) and calculated the area as the surface of a hemisphere ($C^2/2\pi$). Coral head area averaged 2.34 m^2 (SD = ±1.97, range = 1-11 m^2). Interspersed among the coral heads were twelve rubble piles each approximately 0.75 m^2 constructed of dead *P. porites* coral. The coral heads and rubble piles were at least 3 m distant from any other reef structure and surrounded by barren sand.

Prior to the start of the experiment, all *Stegastes* species were removed using hand nets and quinaldine, an anesthetic. Half (n = 6) of the coral heads and half of the rubble piles at each site were randomly selected to receive adult bicolor damselfish (30 mm to 50 mm standard length) at $3/m^2$ which was the natural density on coral heads in this area. The remaining experimental units received no adult fish. There were six replicates of each treatment per site for a total of 48 experimental units.

At EFR all newly settled *S. partitus* were collected every one or two days for 30 d from each experimental unit and preserved in 70% EtOH. At WFR experimental units were censused for new recruits every two to four days. All surviving recruits were collected and preserved in 70% EtOH when the study was terminated. This experimental design, where settlers were collected at one site and recruits monitored at another, was selected to avoid the possibility of recruits moving from coral heads or rubble piles with many fish to those experimental units where all settlers were removed daily. Although this design may be considered pseudoreplicated, I assumed that larvae settling to both sites (about 100 m apart) were of the same cohort and did not differ in their larval history. This experiment was designed to simultaneously test for the effects of substrate type and presence of conspecific

adults on settlement and recruitment patterns, and for the effect of larval size and age on settlement behavior and post-settlement growth and survival.

Larval Size, Age and Growth from Otoliths

The collections of settlers at EFR yielded size and age at settlement, and the collections of recruits at end of experiment at WFR yielded size and age at settlement of survivors. Thus, comparison of larval size and age at settlement between newly settled larvae and surviving recruits was possible. Preserved fish were measured to the nearest 0.5 mm standard length (SL) and weighed to the nearest 0.01 g before otoliths were extracted. Lapillar otoliths were lightly polished on 4000 grit paper then permanently mounted on glass slides with cyanoacrylate glue. The lapillus with the clearest ring structure was viewed on a compound microscope at 400x or 600x magnification using polarized light and immersion oil. Daily otolith increments are created by diel cycles of calcium deposition during growth as benthic juveniles (Victor 1986) and it was assumed that increments were formed daily during the planktonic larval stage as well.

In many fish the wider pre-settlement increments are separated from the narrower post-settlement increments by a transition in otolith microstructure, the settlement mark (Brothers et al. 1976; Victor 1982; Pitcher 1988). In the bicolor damselfish the average width (± 1 SD) of pre-settlement increments, settlement mark and post-settlement (for fish <30 d old) increments were 8.5 μm (±0.85), 25.0 μm (±7.95), and 4.0 μm (±0.75), respectively. Larval duration was calculated by counting the wider series of bands from the settlement mark to the lapillus nucleus as described by Victor (1982). In addition BioScan® Optimas imaging software was used to digitally

mark, count and measure the width of otolith increments. The width of presettlement and postsettlement increments was used as an estimate of daily growth rate during larval and post-larval periods (Pannella 1971; Victor 1986, 1987, 1991). The relationship between fish length and lapillus radius was linear and strongly correlated (Fig. 1) and can be expressed as

Standard length (mm) = 0.0561(otolith radius(μm)) - 1.776.

I used this equation to estimate fish size at any age by measuring the distance from the otolith nucleus to the corresponding otolith increment.

Post-Settlement Growth and Survivorship

The influence of larval supply on population structure was examined by comparing the proportion of juvenile and adult *S. partitus* among back reef and fore reef zones in Teague Bay during July in 1991, 1992, 1993 and 1994. Juvenile (i.e. recruitment) and adult densities were visually sampled by SCUBA divers who swam at a constant speed along randomly placed 30 x 1 m strip transects. Divers held a 1 m wide T-shaped bar for reference and counted all juvenile or adult fish that passed within the sampling area. Since the fore reef slope is much larger in area than the back reef slope (see Methods: Study Site), transects on the fore reef were conducted at three separate locations to get a more representative sample of population structure. It was calculated that at least 16 juvenile fish transects were required to minimize variation in counts of recruits among locations whereas eight transects were sufficient for adult damselfish.

The experimental design to examine postsettlement effects on population structure consisted of four replicate *M. annularis* coral heads (1 to 1.25 m^2) and *P. porites* rubble piles (1 m^2) isolated in sand flats in adjacent

fore reef and back reef zones. These sites were located about halfway between EFR and WRF described above. The 16 experimental units were denuded of all other fishes and juvenile bicolor damselfish were removed from adjacent substrates to eliminate potential immigration onto experimental units. Each experimental unit received equal densities (4 fish/m^2) of juvenile *S. partitus* which had been tagged with tattoo ink and treated in a 0.25 g/l bath of tetracycline hydrochloride for 12 hr to mark their otoliths (Hettler 1984; Schmitt 1984; Fowler 1990; Alcobendas et al. 1991; Hendricks 1991).

The mean standard length (mm ± 1 SD) of fish stocked on each replicate was: back reef coral (14.3 ±1.14, N = 16, range = 13-17 mm) and rubble (13.8 ±1.45, N = 18, range = 12-17 mm), and fore reef coral (14.1 ± 2.52, N = 18, range = 12-22 mm) and rubble (14.1 ±1.81, N = 16, range = 12-20 mm). Once established on the experimental units, the fish remained for the duration of the 13 d experiment. This was verified during periodic censuses for emigrants into the surrounding area. In only two instances, once on the back reef and once on the fore reef, was an experimental fish found on an adjacent coral head. This occurred within the first two days after stocking so each fish was recaptured and returned to the nearest experimental unit, a coral head. The number of potential predators were also censused twice in an area approximately 100 m^2 around the study site. The maximum number counted during any one census was used to estimate its abundance in the area.

During the two week study, feeding behavior and aggressive interactions (chases and flees/min) were recorded for each fish during three 10 min observation periods. Feeding behavior included feeding rate (bites/min) and feeding habitat: plankton and benthic (included feeding on bare rubble, algae, sand, live coral, sponges and polychaete fan worms). Aggressive interactions between target individual and all other species were categorized as chasing or

fleeing by a larger or smaller fish. A total of 57 hours of behavioral observations was recorded from fish surviving on the fore reef (n=22) and back reef (n= 20) between 15 and 26 August from 08:30 to 18:30. To compare behavior of tetracycline treated fish with the behavior of unmanipulated fish, an additional 21.5 hours of observations were conducted on 15 individuals which had naturally recruited to WFR (see Methods: Settlement and Recruitment Experiments).

At the end of two weeks, surviving fish were collected and their otoliths extracted and examined for a tetracycline mark. Four fish did not have the mark (recruited from plankton) and were removed from further analysis. The tetracycline mark identified the date of release whereas the distance from the mark to the edge of the otolith identified the growth incurred during the study. Lapilli were viewed under UV illumination and growth was measured from a digitized image calibrated to the appropriate magnification. Lapillus radius was found to be highly correlated with standard length of fish (r^2=0.90) and thus was a good predictor of individual growth rate (Fig. 1). The formation of daily growth increments on otoliths has been experimentally verified for the bicolor damselfish by Robertson et al. (1988) but was confirmed by counting the number of increments from the tetracycline mark to the edge of the lapillar otolith for all fish.

Statistical Analysis

All statistical analyses were performed using the MGLH or STATS program of SYSTAT (Wilkinson 1990)and significance levels were set at alpha = 0.05. Prior to analyses data were tested for homogeneity of variances using Bartlett's chi-square (Sokal and Rohlf 1981). When necessary ($p<0.05$ for

Bartlett's test) data were transformed ln(X + 1) to meet assumptions of homoscedasticity.

Settlement and recruitment patterns were analyzed with analysis of variance (ANOVA) using total settlement (sum of all fish) and total recruitment (last census), respectively, as dependent variables and presence of conspecific adults and substrate type as main effects. A t-test compared larval duration of settlers and recruits for 1992 and 1994. Differences in size at settlement between settlers and recruits were tested with an analysis of covariance since larval otolith radius covaried positively with larval age. The effects of larval size and age on settlement preferences for different substrates and presence of adults were also examined using ANOVA. The size and age of fish settling on each experimental unit at EFR were averaged to yield a single length and age per replicate. Sample sizes from the recruitment portion of study (WFR) were too small for analysis. Pre- and post-settlement growth rates using otolith increments were compared with regression.

Juvenile growth rates, foraging rates and aggressive interactions of tetracycline treated fish were averaged for each experimental unit to yield a single datum point for each unit thus avoiding pseudoreplication (Hurlburt 1984). Since size may affect growth and behavior, these data were analyzed using two-way analysis of covariance with zone (fore and back reef) and substrate type (live coral and coral rubble) as fixed factors and standard length as a covariate. The number of fish surviving on experimental units was converted to proportions, arcsin square root transformed (Sokal and Rohlf 1981) and analyzed with ANOVA. Census data on juvenile and adult abundances in back and fore reef zones were averaged for each year (n=4) and analyzed with ANOVA.

RESULTS

Effects of Larval History on Settlement

Size and age at settlement. Otolith microstructure was analyzed for all settlers and surviving recruits that were collected in 1992 and 1994. Average post-settlement age (± 1 SD) of recruits was 19.7 d (±9.229, range = 0-40 d) in 1992 and 21.6 d (±11.96, range = 8-45 d) in 1994. This indicates that most recruits used in the analyses had survived the first few critical weeks of life on the reef.

Mean larval duration and size at settlement did not differ significantly between settlers collected daily (EFR) and surviving recruits (WFR) in 1992 or 1994, nor did it differ between years (Table 1). Size at settlement of surviving recruits was estimated (back-calculated) from their otolith radius and were compared to fish collected at settlement. Since larval size and age at settlement were similar among years, these data were combined to examine length/age relationships of larvae. A positive correlation was found between larval size and age at settlement ($F_{1,73} = 26.37$, $R^2=.27$, $P<0.001$) but this relationship was relatively weak (Fig. 2).

Presettlement and postsettlement growth. The width of daily otolith increments provided an estimate of larval growth rates throughout the pelagic phase in addition to growth rates in the days following settlement. Larval growth rates fluctuated throughout the pelagic phase but showed a marked decrease beginning on about day 18 and continued until settlement (Fig. 3a). This probably contributed to some of the scatter seen in Figure 2. There was a significant difference ($F_{1, 41} = 11.14$, $P = 0.002$) in the average width of otolith increments between early larval life (day 6 to 10 post-

hatching, 9.5 μm ± 1.50 SD) and the last 5 days before settlement (8.0 μm ± 1.0 SD).

Table 1. Average planktonic duration and size at settlement of daily settlers and surviving recruits collected in 1992 and 1994. All pairwise comparison of size and age of settlers and recruits within years, and pairwise comparison between years were non-significant at $p<0.05$.

	N	Larval Duration		Length at Settlement	
		range (d)	age (±1 SD)	range (mm)	size (±1 SD)
1992					
Settlers	46	18 - 29	23.8 (2.671)	10 - 14.5	12.0 (1.00)
Recruits	24	20 - 33	23.7 (2.761)	10.5 - 13	11.8 (0.58)
1994					
Settlers	29	18 - 31	24.7 (3.313)	10 - 14	12.2 (0.88)
Recruits	9	22 - 27	24.0 (1.658)	11.5 - 13.5	12.3 (0.56)
YEAR					
1992	70	18 - 33	23.8 (2.684)	10 - 14.5	12.0 (0.87)
1994	38	18 - 31	24.6 (3.001)	10 - 14	12.2 (0.81)
TOTAL	108	18 - 33	24.1	10 - 14.5	12.0 (0.86)

Larval growth rates soon after hatching had a strong effect on larval duration. Larval growth rates of fish with planktonic durations within approximately one standard deviation of the mean (23.8±2.68 = 22-26 d) were compared to fish that were both younger (18-21 d) and older (27-33 d) at settlement. Fish that settled at a younger age had significantly greater growth rates during the first third of their larval life than fish experiencing longer larval durations (Table 2, Fig. 3 b). The weighted averages (50%) of these curves show the relationship more clearly (Fig. 3c). The width of otolith increments of young and old larvae converged after the period of maximum growth.

Increase in fish length during the planktonic stage (calculated from daily otolith increment widths) was significantly greater for the youngest age class of larvae (Table 2). Based on these estimates, I calculated the growth trajectories from hatching (2.1 mm) to settlement for the three age classes. These trajectories accurately estimated the minimum size and age of young (10 mm, 18 d), average (10.5 mm, 22 d) and old (11 mm, 27 d) bicolor damselfish larvae (Fig. 4). Larval growth rates also had a significant effect on postsettlement events. Larvae that had fast growth rates just before settlement continued growing faster than average after settlement ($F_{1, 20}$ = 14.73, P = 0.001, Fig. 5). Larval age at settlement, however, had no effect on postsettlement growth ($F_{1, 20}$ = 0.23, P = 0.634).

Table 2. Differences among young (y), average (a) and old (o) *S. partitus* larvae. Average aged larvae are approximately 1 standard deviation from the mean age (23.8 d ± 2.68). ANOVA tested for differences in growth among age classes using average otolith increment width (μm) during larval days 2-6 and days 13-18. Standard errors of the mean are in parentheses. N is number of fish in each age class. Grouped letters (y,a,o) indicate ns differences in Tukey mean comparisons. Average daily growth rate (mm SL/d) and size at settlement were also analyzed but used only those fish collected at settlement (n = 11, 26, 9 for y, a, o).

	Age Group			Statistical Analysis		
Parameter	18-21 (y)	22-26 (a)	27-33 (o)	F	P	Tukey
N	20	36	13			
Inc. width (day 2-6)	9.89 (1.25)	8.96 (1.82)	7.77 (1.05)	7.429†	0.001*	ya, ao
Inc. width (d 13-18)	9.06 (0.96)	9.32 (0.90)	8.34 (1.14)	4.916†	0.010*	ay, yo
Growth (mm/d)	0.47 (0.06)	0.41 (0.04)	0.39 (0.05)	7.314‡	0.002*	y, ao
Size at settlement	11.7 (1.01)	12.0 (0.89)	12.5 (1.20)	1.586‡	0.216	yao

† d.f. = 2, 66.
‡ d.f. = 2, 43.

The effect of larval history on larval preferences at settlement was also examined. Due to the low number of recruits collected at WFR in 1992 and low overall settlement in 1994, this analysis included only those fish collected at settlement (EFR) in 1992. Larvae selecting coral substrate were larger than larvae settling on rubble (12.5 mm ± 0.293 SE vs. 11.8 mm ± 0.096 SE, $F_{1, 15} = 5.80$, $P = 0.029$). There was no relationship between presence of adults and length of larvae at settlement, nor was there any effect of larval age on settlement preference.

Settlement and Recruitment Patterns

The settlement and recruitment experiments conducted on the fore reef of Teague Bay in 1992 and 1994 revealed that larval behavior at settlement determined initial distribution patterns of the bicolor damselfish and that differential survival after settlement enhanced these initial patterns. Spatial patterns were significantly affected by coral substrate but not the presence of conspecifics. *Stegastes partitus* had significantly greater settlement on *Porites porites* rubble than on *Montastrea annularis* coral heads in both 1992 and 1994 (Table 3, Fig. 6). Presence of conspecifics had no significant effect in either year although fish tended to settle more often without adults on rubble during 1992. As with settlement, recruitment density was greater on rubble in both 1992 and 1994 (Table 3, Fig. 7). Presence of adults showed no significant effect on recruitment, measured as persistence of individuals over the study period (Table 3).

Table 3. Results from two-way ANOVA of the effects of substrate (*Montastrea annularis* coral or *Porites porites* rubble) and conspecific adults (presence or absence) on daily settlement and recruitment of *S. partitus* on the fore reef of Teague Bay, St. Croix USVI for 1992 and 1994.

1992		Settlement			Recruitment		
Source	df	ms	F	P	ms	F	P
Substrata (S)	1	3.375	1.254	0.017*	22.042	29.719	<0.001*
Adult (A)	1	18.375	6.827	0.276	0.042	0.056	0.815
S x A	1	7.042	2.616	0.121	0.042	0.056	0.815
Error	20	2.692			0.742		
1994		Settlement			Recruitment		
Source	df	ms	F	P	ms	F	P
Substrata (S)	1	7.042	4.942	0.038*	3.375	9.00	0.007*
Adult (A)	1	0.042	0.029	0.866	0.375	1.00	0.329
S x A	1	0.375	0.263	0.614	0.375	1.00	0.329
Error	20	1.425			0.375		

* F ratios interpreted as significant at $p<0.05$.

Effects of Post-settlement Processes on Recruitment

Population structure. Visual censuses of *S. partitus* on the back and fore reef of Teague Bay found that adult density was generally greater than juvenile density on the fore reef whereas the reverse was true on the back reef (Fig. 8). Over the four years respective juvenile and adult densities (± 1 SE) averaged 1.4 (±0.51) and 0.3 (±0.16) fish/30 m^2 on the back reef, and 2.5 (±0.52) and 5.0 (±0.074) fish/m^2, on the fore reef. Adult *S. partitus* densities were significantly different between fore reef and back reef ($F_{1, 4} = 43.79$, $p=0.003$) whereas recruitment rates did not differ among zones ($F_{1, 6} = 0.57$, $p=0.478$).

Post-settlement growth. Growth rates of juvenile *S. partitus* living on the fore reef were nearly double the growth rates of fish living on the back

reef (Table 4, Fig. 9). There was no detectable difference in fish growth among substrate type (live coral head vs. rubble pile) in either zone (Table 4). Growth of these experimental fish was calculated by measuring the otolith increment widths before and after fish were manipulated. The tetracycline mark on the otolith indicated the date fish were transferred to experimental treatments. Increase in standard length (SL) of fish was calculated to provide a more relevant measure of growth. For a given age, fish on the fore reef were over 2 mm longer than fish on the back reef (Figure 10). The average SL of fish from each experimental unit at the end of the study differed significantly ($T_{1,14}$ = 3.443, $p<0.01$) between fore reef and back reef: 19.2 mm (±2.14, N = 8, range = 16-24) and 15.2 mm (±1.21, N = 14, range = 13-18), respectively. This yielded growth rates of 0.41 mm/d (±0.117 SD) for fish on the fore reef and 0.094 mm/d (±0.0792 SD) for fish on the back reef and represented a 2.89 % increase in SL per day for fore reef fish and a 0.67 % increase in SL per day for back reef fish. I also calculated growth rates based on the increase in otolith radius (μm/d) and converted this measure to increase in SL (mm/d) using the regression equation from Figure 1: SL = (-1.776 + 56.1 x otolith radius) x 0.001. Total increase in lapillus radius averaged 4.153 μm/d (±0.145) for fish on the fore reef and 2.360 μm/d (±0.188) for fish on the back reef. Growth rate in SL was calculated to be 0.23 mm/d (±0.017) for fish on the fore reef and 0.16 mm/d (±0.014) for fish on the back reef. The discrepancy in SL growth rate between the two methods probably resulted from the negatively allometric relationship between growth of lapillus and standard length of fish (fore reef: $y = -0.262x + 6.964$, back reef: $y = -0.328x + 10.092$). Moreover, if the smaller or slower growing fish on the fore reef experienced greater mortality, then the size of the surviving fish will be skewed toward larger individuals.

Table 4. A) Mean increase (+1 SE) in otolith radius (μm) used to estimate growth rates of *S. partitus* juveniles living on either *Porites* rubble or *M. annularis* coral substrates in the fore or back reef. N = number of fish which had a visible tetracycline mark on their otoliths. B) Results of analysis of covariance of standard length (covariate), habitat (fore or back reef) and substrate (coral or rubble) on mean growth.

A	N	Growth (μm)
Fore Reef		
Coral	8	4.095 (0.221)
Rubble	13	4.212 (0.170)
Back Reef		
Coral	4	2.125 (0.305)
Rubble	11	2.496 (0.194)

B

Source	F	P
Habitat (H)	41.51	<0.001*
Substrata (S)	1.06	0.326
H x S	1.20	0.300
Length	18.78	0.001*

* F ratios interpreted as significant (df = 1, 12).

Behavioral interactions. Differences in growth among fore reef and back reef fish may have resulted from differential ratios of energy acquired (quantity and/or quality of food resources) versus energy expended (defense of territory and other activities). Behavioral observations were utilized as a means of identifying the benthic processes affecting the demographic rates of these juvenile bicolor damselfish on each side of the reef. Before these data were compared analyses of behaviors between tetracycline-treated fish and fish which recruited naturally revealed no differences in feeding rates (planktonic: $F_{1,35} = 0.01$, $P = 0.923$, benthic: $F_{1,35} = 0.66$, $P = 0.422$) or in aggressive interactions (intraspecific: $F_{1,35} = 0.01$, $P = 0.927$, interspecific: $F_{1,35} = 0.26$, $P = 0.611$, interfamilial: $F_{1,35} = 0.63$, $P = 0.433$). This indicated that

manipulated fish were behaving normally. The following analyses, however, do not include the behavioral data from the naturally recruited fish.

Foraging rates (bites per min) among experimental treatments were compared for planktonic and benthic feeding categories. Fish living on coral heads fed at significantly higher rates in the plankton than fish living on rubble. Benthic feeding rates were similar among zones and substrate types (Table 5A, B). Time budget of feeding behaviors indicated that fore reef fish spent 70% of their foraging time feeding on planktonic organisms whereas back reef fish spent only 45% of their time feeding in the plankton ($F_{1,12}$ = 9.443, P = 0.01). However, when fish length was included in the analysis as a covariate the effect of reef zone on foraging behavior became nonsignificant (Table 5B).

Territorial defense was quantified by observing the number of times experimental fish would either chase or be chased by other fishes. Rates of attacking or fleeing were combined to get total aggressive encounters. During the preliminary analysis several natural groupings relevant to degree of niche overlap (Ebersole 1977) became apparent. Thus, data were grouped as intraspecific aggression (adult and juvenile bicolor damselfish), interspecific aggression (all other *Stegastes* spp.) or interfamilial aggression (all other non-pomacentrid spp.). Level of intraspecific aggression was elevated for juvenile *S. partitus* on the fore reef due to the presence of several adult *S. partitus* which moved onto experimental units (Table 6A, B). Conversely, the frequency of interspecific aggressive encounters was higher on the back reef primarily with *S. leucostictus* but also *S. planifrons*. Rates of aggression with non-pomacentrid species were similar among all treatments (Table 6A, B).

Table 5. A) Mean (+1 SE) planktonic and benthic foraging rates (number of bites per minute) of *S. partitus* juveniles living on either *P. porites* rubble or *M. annularis* coral substrates in the fore reef or the back reef. N = number of fish observed. B) Results of analysis of covariance of standard length (covariate), habitat (fore and back reef) and substrate (coral and rubble) on foraging rate. Benthic foraging data were transformed ln(X + 1) to meet the assumptions of homoscedasticity.

A	N	Planktonic	Benthic
Fore Reef			
Coral	8	6.67 (±1.081)	1.21 (±0.138)
Rubble	14	1.93 (±0.363)	1.50 (±0.404)
Back Reef			
Coral	5	3.78 (±1.631)	2.10 (±0.582)
Rubble	15	1.78 (±0.081)	3.58 (±0.852)

B

	FORAGING					
	Plankton		Benthic		% Time in Plankton	
Source	F	P	F	P	F	P
Habitat (H)	0.37	0.555	3.59	0.085	3.69	0.081
Substrata (S)	10.62	0.008*	1.74	0.214	8.96	0.012*
H x S	1.50	0.247	0.57	0.470	0.12	0.738
Length	0.51	0.491	0.04	0.849	0.02	0.886

* F ratios interpreted as significant (df = 1, 11).
†Higher order interactions in analysis were non-significant at $p<0.05$.

Mortality and migration. Migration of juvenile *S. partitus* off the experimental units was minimal. Since the surrounding area was denuded of all juvenile *S. partitus* prior to the experiment, detection of tattooed migrants was relatively simple. Only two juveniles emigrated from experimental units during the first two days of the study and these were replaced onto the nearest unit, a coral head. Although mortality during or after migration could not be accounted for, disappearance of fish from experimental units was attributed to mortality.

Table 6. A) Mean (+1 s.e.) aggressive interactions (number of attacks and flees per minute) of bicolor damselfish with other *S. partitus* (intraspecific), with other *Stegastes* spp. (interspecific) and with non-pomacentrid spp. Juveniles were living on either *P. porites* rubble or *M. annularis* coral substrates in fore reef or back reef habitats. N is number of fish observed. B) Results of analysis of covariance of standard length (covariate), habitat and substrate on aggression (intraspecific, interspecific, other spp.). Intraspecific and interspecific aggression data were transformed ln(X + 1) to meet the assumptions of homoscedasticity.

A	N	*S. partitus*	*Stegastes* spp	Other spp.
Fore Reef				
Coral	8	0.22 (0.184)	0.02 (0.017)	0.07 (0.020)
Rubble	14	0.24 (0.115)	0	0.01 (0.007)
Back Reef				
Coral	5	0	0.35 (0.223)	0.08 (0.075)
Rubble	15	0.16 (0.043)	0.11 (0.032)	0.03 (0.011)

B

	AGGRESSION							
	Intrasp.		Intersp.		Other spp.		Total	
Source	F	P	F	P	F	P	F	P
Habitat (H)	5.33	0.03*	10.89	0.01*	0.08	0.78	0.73	0.41
Substrata (S)	1.03	0.33	1.60	0.21	1.60	0.23	0.37	0.56
H x S	0.32	0.58	0.20	0.66	0.09	0.76	0.01	0.92
Length	2.23	0.14	0.62	0.44	0.70	0.42	3.20	0.10

* F ratios interpreted as significant (df = 1, 12).
†Higher order interactions in analysis were non-significant at $p<0.05$.

Fish were censused once during the study and all remaining fish were collected at the end of the study as an estimate of mortality. Percent survival was greatest for fish living on the fore reef in rubble substrate (87.5%). The next highest survival occurred for fish living on rubble in the back reef (61%), followed by fish living on coral on the fore reef (44%). Lowest survival was for fish inhabiting coral on the back reef (25%). The analysis of variance with zone and substrate as main effects indicated that both reef zone ($F_{1,8} = 10.46$, $P = 0.007$) and substrate type ($F_{1,8} = 16.44$, $P = 0.002$) were important in affecting mortality rates of *S. partitus* juveniles (Fig. 9). The interaction term was not

significant ($F_{1,8} = 1.48$, $P = 0.248$). Census of potential predators in the back and fore reef zones suggested that predators differed little in number and type (Table 7). What effect these predators had on the different size classes of bicolor damselfish is unknown. Overall, *S. partitus* mortality rates in the back reef of Teague Bay were more important than recruitment in determining adult population density. On the fore reef where recruitment rates were slightly higher and total mortality rates considerably lower, population abundance was affected more by recruitment than benthic mortality.

Table 7. Maximum number of potential predators seen over two censuses around experimental units used in study. Census area was approximately $100m^2$ in fore and back reef. Categories include groupers (*Epinephelus guttatus*), small serranids (*Serranus tigrinus, S. tabacarius, Hypoplectrus* spp.), lizard fish (*Synodus intermedius*), moray eels (*Gymnothorax moringa*) and trumpetfish (*Aulostomus maculatus*).

Reef Habitat	Large Grouper	Small Serranid	Lizard fish	Moray eel	Trumpet fish
Fore reef	3	3	3	1	0
Back reef	2	6	0	1	1

DISCUSSION

In marine fishes, the planktonic larval phase, the transition to the benthic juvenile form and the period preceding maturity each impose a unique set of constraints that limit an individual's ability to successfully reach adulthood and reproduce. The cumulative effects of these constraints will, in turn, influence the distribution patterns and abundance of the juvenile and adult population. Integrating these components of complex life histories is necessary to fully understand the importance of each stage.

Variation in Growth During Larval Life

Based on the width of otolith increments, the estimated growth rates of larval bicolor damselfish varied considerably from hatching through settlement. In general, growth rates increased to a maximum 10 to 15 d after hatching then showed a marked decrease beginning around day 18 and continuing until settlement. The trend of increasing then decreasing otolith increment width is similar to that described for the bluehead wrasse (*Thalassoma bifasciatum*) by Victor (1986). Day 18 in the life of *S. partitus* corresponds to the youngest and smallest (10 mm SL) fish collected at settlement indicating that competence to settle may occur at this size and age. This is the first documented case of a pomacentrid showing such reductions in larval growth. Reduction in larval growth rates at competency and the ability to delay settlement and metamorphosis has long been known to occur in marine invertebrates (Thorson 1950) and has recently been described in marine fishes (Cowen 1991; Victor 1986c). Slowed growth at competency may be an adaptive response to maintain small size, perhaps because large planktonic larvae may experience greater mortality due to physiological factors (Scheltema 1971; Pechenik et al. 1984) or are at greater risk of predation (Litvak and Leggett 1992).

The ability to delay metamorphosis and the resultant flexibility in the timing of settlement may be an adaptation for maximizing the return of planktonic larvae to coastal waters (Jackson and Strathmann 1981; Victor 1986). This hypothesis assumes that larvae with long larval durations exist because they have drifted far from shore and have not received the correct cue for settlement and metamorphosis. Marine fish larvae that hatch from

pelagic spawned eggs (e.g. Labridae) tend to disperse into waters farther offshore (up to 1200 km, Leis 1983) than larvae hatched from demersal eggs (e.g. Pomacentrids). Plankton transects from the Great Barrier Reef lagoon to 15 km offshore into the Coral Sea found most pomacentrid larvae within 1 km of shore or in the lagoon. In contrast, labrid larvae were equally abundant from 1 to 15 km off shore (reviewed by Leis 1991). These distribution patterns would suggest that the ability to delay metamorphosis would greatly benefit pelagic spawners but be less important for demersal spawners since they tend to be closer to shore. It follows that variation in settlement age of pelagic spawners may be largely due the presence or absence of a settlement cue at competency. Alternatively, I suggest that, for demersal spawners, variation in growth rates early in larval life (<10 d post hatching) largely determine planktonic duration. While the settlement cue may be ever-present for larvae in near-shore waters, the age and size at which competency is achieved will depend upon the initial rate of growth and development. Moreover, recent evidence suggests that competent larvae have the ability to quickly swim to a reef over 1 km away (Stobutzki, pers. comm.). Enhanced larval development together with a strong behavioral component provide the mechanisms to facilitate early settlement.

An increased rate of growth early in the life of bicolor damselfish larvae (early-stage larvae) reduced the time required to reach competency and the age at which they settled (Fig. 3c). Whether these elevated growth rates for some individuals reflected differences in morphological development (e.g. synchronized development of jaw morphology), larval feeding behavior (e.g. superior prey recognition and capture) or environmental variability (e.g. rich food patch encountered) is unknown. Functional morphological studies have shown that larval fishes pass through several critical stages in the

development of their feeding apparatus (Liem 1991). In pomacentrids (e.g. *Amphiprion* spp.) and cichlids (*Haplochromis elegans*) the transition from the hyoid stage to the opercular stage is important in switching from "ram" to the more efficient "suction" mode of feeding (Otten 1982; Liem 1991). In *Amphiprion,* major remodeling of strategic musculoskeletal elements ("hot spots") occurs during the first eight days post-hatching and is associated with large amounts of variation among individuals of the same size class (Dilling 1989; Liem 1991). Variation in the speed and efficiency of this restructuring will allow certain individuals to utilize food resources earlier than other larvae leading to differential rates of growth.

Variation in larval feeding behavior in the first few days of pelagic life may also cause large differences in growth rate. Percent feeding success of many species of temperate marine fishes increase dramatically from day 2 (20%-70% success) to day 15 (85% - 95% success) posthatching (reviewed by Blaxter 1986). Coughlin (1992) described *Amphiprion* larvae to have extremely variable success in capturing *Artemia* nauplii in the first 3 days after hatching. This was largely due to their inability to synchronize their attack with the positioning and opening of their jaws. Pelagic larvae learning to feed in the ocean will encounter a greater diversity of prey which may enhance or reduce feeding efficiency relative to laboratory reared fish.

A third alternative involves the environmental variability of food supply. Concentrated patches of food provide a greater net gain in energy because fish will spend less time searching and more time feeding than in an area where food was dispersed less contagiously. Northern anchovy larvae (*Engraulis mordax*) reduced their swimming speed and fed in a smaller area when in dense food patches than larvae outside of these patches (Hunter and Thomas 1974). More recent evidence was provided by McCormick and

Molony (1992) who found that goatfish larvae (*Upeneus tragula*) grew faster when fed *Artemia* nauplii continuously every day (f1) or starved for 3 d then fed continuously thereafter (f2) than larvae fed once every day (f3) or every second day (f4). Fish which grew the fastest (feeding treatment f1 > f2 > f3 > f4) settled at an earlier mean age (14 d < 16 d < 22 d < 24 d, respectively). Slow growth has been shown to increase time to settlement in temperate species as well (Chambers and Leggett 1987). Hydrological features such as convergence zones (tidally induced fronts, Langmuir circulations) are spatially and temporally variable phenomena which concentrate zooplankters (Kingsford 1990; Kingsford et al. 1991). These localized oceanographic features may contain an order of magnitude greater density of larval food than adjacent waters (summary by Kingsford 1990). Larvae that feed in these slicks soon after hatching may gain a distinct advantage over those that do not. Methot and Kramer (1979) found the growth rates (based on otolith increments) of anchovy larvae (*E. mordax*) to be highly variable among stations a few nautical miles distant. Given the spatial and temporal patchiness of food in the ocean, one could expect larval survival and growth to reflect a similar patchiness (i.e. variability) within a relatively small area (Hunter 1981).

The ability to procure food quickly and efficiently in the ocean will depend on the ability of fish larvae to locate, pursue and capture prey. Variations in these abilities, especially in the early stage larvae of demersal spawners, will cause differential rates of growth among individuals. My data suggest that differential growth rates in early stage larvae establish canalized trajectories toward larval competence and provide a mechanism for determining planktonic duration (Figure 3c, 4). The alternatives discussed above offer testable hypotheses for future studies to determine the relative importance of intrinsic versus extrinsic factors in early stage growth rates.

Effects of Larval History on Postsettlement Events

Pelagic larvae with different presettlement histories may have greater or lesser abilities to successfully make the transition to the benthic environment (Connell 1961; Labelle and Nursall 1985; Cowen 1991; McCormick and Molony 1992). Variability in age may indicate differences in developmental state whereas variability in size at settlement will affect swimming efficiency and vulnerability to predation. For the bicolor damselfish, as with other pomacentrids (Thresher et al. 1989), its larval stage is relatively short giving rise to a narrower range in size and age at settlement than other marine fish species (Bigelow and Schroeder 1953; Laurence 1975; Markle 1975; Policansky 1982, 1983; Brothers 1983; Victor 1986; Chambers and Leggett 1987). The size (SL) of newly settled *S. partitus* collected in this study (mean = 12.1 mm, range = 10 - 14.5 mm, n=75) was comparable with earlier studies in St. Croix, [mean = 12.8 mm, range = 10.7-14.9 mm, n = 14; (Wellington and Victor 1989)] and Panama [mean = 13 mm, range = 10.4-15 mm, n = 206; Robertson et al. (1988)]. Planktonic durations (mean = 23.8 d, range = 18 - 33 d; this study), were similar to those found by Wellington and Victor (1989) (mean = 28.8 d, range = 27 to 31 d) but were considerably shorter than those found by Robertson et al. (1988) (mean = 36.5 d, range = 31 to 45 d). These data suggest that planktonic duration can be quite variable among locations but that larval size is probably constrained to a relatively narrow range. This was quite apparent in my study where 8 days but only 0.8 mm separated the mean age and mean length of young and old larvae. Calculating growth trajectories from new recruits collected at various locations throughout a species'

geographical range may provide a method of explaining some of the variation in settlement age among populations.

Do these variations in larval duration, growth and size at settlement influence pre- and postsettlement survival? Litvak and Leggett (1992) found that being smaller at a given age actually conferred a survival advantage to pelagic capelin larvae (*Mallotus villosus*). Piscivore foraging behavior seemed to focus on the larger and more active larvae. Chambers et al. (1988) and Cowen (1991) suggested that species that delay growth in the plankton may be able to compensate by increasing growth rates upon settlement. This was verified for laboratory reared winter flounder (*Pleuronectes americanus*) by Bertram et al. (1993) who followed growth of larvae up to 7 wk after metamorphosis. McCormick and Molony (1992) provided alternative evidence from field caught goatfish larvae (*U. tragula*) that individuals that were well fed during the larval stage were larger, settled earlier and continued growing faster after metamorphosis than did slower growing larvae. In my study, increased rates of larval growth prior to settlement (late-stage larvae) seemed to span metamorphosis and continue in the settled individual for at least 2 weeks (Fig. 5).

In the benthic environment, large size and faster growth rates may confer a survival advantage. Fish settling at a smaller size may experience elevated predation rates due in part to reduced swimming abilities relative to larger fish and, more importantly, due to increased vulnerability to a wider range of potential predators (Jeffries and Terceiro 1985; McCormick and Molony 1992; Juanes 1994). Contrary to these studies, Bertram and Leggett (1994) found no effect of size or age on survivorship of postlarval *P. americanus* to an invertebrate predator. The results of my settlement and recruitment study also showed that size and age at settlement had no effect on

survivorship of the bicolor damselfish. However, I found that settlement by larvae onto different substrates and into different habitats had a substantially greater effect on post-settlement survival than larval history.

Consequences of Larval Decisions at Settlement

Differential mortality in the benthic environment can be affected both directly, due to architectural characteristics of the substrate (see Chap. 2), and indirectly due to subsequent juvenile growth rates. The settlement and recruitment experiments conducted in this study revealed that within a habitat larval settlement behavior was important in determining small-scale (10's of m) distribution patterns of *S. partitus* and that differential survival after settlement enhanced these initial patterns. Bicolor damselfish larvae preferentially selected coral rubble 3:1 over live *Montastrea annularis* coral heads even though *M. annularis* colonies dominate the Teague Bay study site. Larger larvae tended to settle on live *M. annularis* coral (12.53 mm SL) heads whereas smaller larvae settled on rubble (11.79 mm SL). These larvae, which were 6.28% larger, may have been responding to their perceived sizes relative to the refuges available in the different substrates. Refuges close to the body size of the individual seem to be the most important factor for minimizing predation risk (Roberts and Ormond 1987; Clarke 1989; Hixon and Beets 1989, 1993; Hunte and Cote 1989.

The architecture of *Porites* rubble consists of an abundance of small holes connected by a complex matrix of tunnels. In contrast, the columnar-lobate (Weil and Knowlton 1994) morphology of *M. annularis* colonies provide a variety of large and small crevices among the fist-sized knobs of living coral. These differences in substrate morphology partly contributed to the

differential persistence of newly settled juveniles. Although the structural architecture of different substrates can largely influence risk of predation (Sale et al. 1980, 1984; Shulman et al. 1983; Kaufman and Ebersole 1984; Shulman 1985; Sweatman 1985a, b; Robertson 1988; Connell and Jones 1991; Hixon and Menge 1991; Hixon and Beets 1993), predator encounter rates will also affect survival. The larger size of crevices on *M. annularis* colonies sheltered a greater diversity of large piscivores than did rubble (pers. obs.). Hixon and Beets (1989, 1993) showed that large piscivorous fishes were more abundant on artificial reefs with larger available holes. This condition resulted in decreased prey abundances on reefs with large holes. More detailed information on the shelter characteristics of naturally occurring substrates may shed light upon why some architecture types enhance survival.

Post-settlement mortality rates were also influenced, albeit indirectly, by differences in juvenile growth. Growth rates of fish living on the fore reef were more than double the growth rates of fish living on the back reef. These dramatic differences in juvenile growth among habitats (back vs. fore reef) influenced post-settlement mortality almost as much as differences in substrate architecture (Fig. 9). Based on growth rates, estimated from otolith increments, a 10 mm recruit would reach sexually maturity (35 mm SL; Schmale 1981; Sadovy 1986) in about 3.5 months if it settled on the fore reef and 7 months if it settled on the back reef.

From my behavioral observations I concluded that reduced growth rates in the back reef were due to the combined effects of differences in preferred food supply relative to the fore reef, and differences in competition for resources (space and food) with other territorial pomacentrids. Different foraging patterns by juveniles among reef zones may have reflected a reduction in planktonic food supply between the fore reef and back reef.

Because of their increasing need for a planktivorous diet as they grow (Emery 1968, 1973), the depletion of planktonic organisms between the fore and back reef (Glynn 1973; Bray 1981; Gaines and Roughgarden 1987; Hamner et al. 1988; Kingsford and MacDiarmid 1988) may have contributed to reducing juvenile *S. partitus* growth rates and limiting abundance of adults (Fig. 8). When adult *S. partitus* were observed on the back reef they were often concentrated along those portions of the reef where the reef crest was relatively narrow and delivery of planktonic food may have been enhanced. In these same locations small aggregations of other highly planktivorous species (*Chromis* spp.) also persisted (pers. obs.). Other studies have found juvenile reef fishes to be food limited as well (Jones 1986; Forrester 1990). Moreover, rates of interspecific aggression on the back reef increased dramatically over time and could have affected individual rates of growth and probability of mortality (Shulman 1985a,b; Booth 1995). This was largely due to immigration and settlement of the pomacentrids *S. leucostictus* and *S. planifrons* onto the experimental reefs. The negative effects of escalated aggression includes increased predatory risk due to reduced vigilance for predators (Jakobsson et al. 1995) and decreased growth due to the greater amount of energy expended.

Constraints on Ontogenetic Variation During Life History Transitions

Complex life cycle theory predicts that conflicting demands will occur at the transition between ontogenetic stages (Istock 1967). Rapid larval growth rates early in the life of *S. partitus* shortened their planktonic duration and may have increased their probability of survival during this vulnerable period (Chambers and Leggett 1987; Rice 1987,1993; Bailey and Houde 1989;

Pepin 1989). However, they were only slightly more common than older larvae at settlement. The "optimum" size/age larvae must be based upon the trade-off between probability of survival in the planktonic environment versus the probability of survival after settlement into the benthic environment. The "optimum" size/age larvae therefore is what remains after the more extreme sizes/ages are culled (Rowe and Ludwig 1991). These ecological constraints may be minimized by selecting habitats at settlement that maximize growth while reducing chance of mortality. However, many species still have generalized habitat preferences (Sale 1977, 1978) and persistence of juveniles in the days following settlement reflects their vulnerability among different microhabitats (Sale and Ferrell 1988; Eggleston and Armstrong 1995). This paper has identified multiple factors and processes which can influence larval history, affect small-scale (10's of m) distribution patterns of newly settled larvae, and possibly influence the large scale (100's of m) distribution and abundance of the adult population. Different growth trajectories among individual larvae and juveniles were very important in determining many of these demographic parameters.

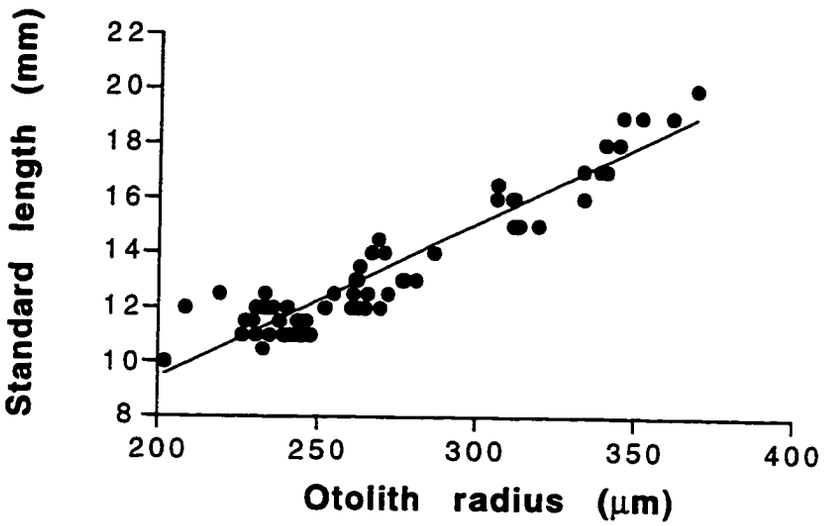

Figure 1. Relationship between standard length (mm) and otolith radius (μm) for 65 juvenile bicolor damselfish. Line fitted with regression analysis, $y = -1.776 + 0.0561x$, $r^2 = 0.90$, $p<0.001$.

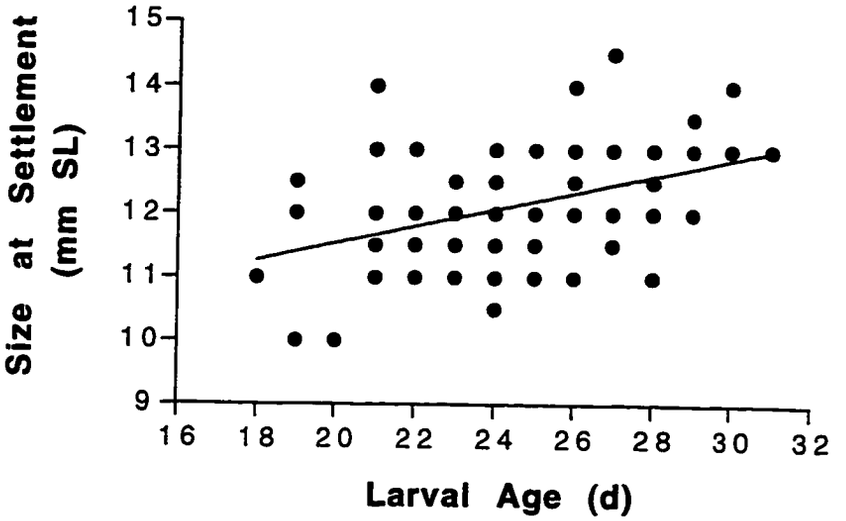

Figure 2. Relationship between standard length (mm) and planktonic duration (d) for 75 newly settled bicolor damselfish. Line fitted with regression analysis, $y = 8.88 + 0.132x$, $r^2 = 0.17$, $p<0.001$.

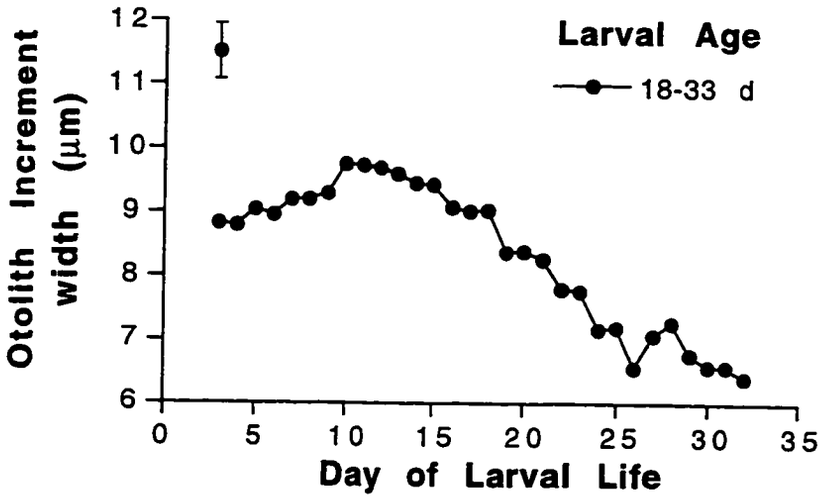

Figure 3a. Daily change in the average otolith (lapillus) increment width during the larval stage of 69 *S. partitus*. Average larval age was 23.8 d (± 2.68 SD, mode = 24). 95% confidence interval of the mean for all days shown in upper left.

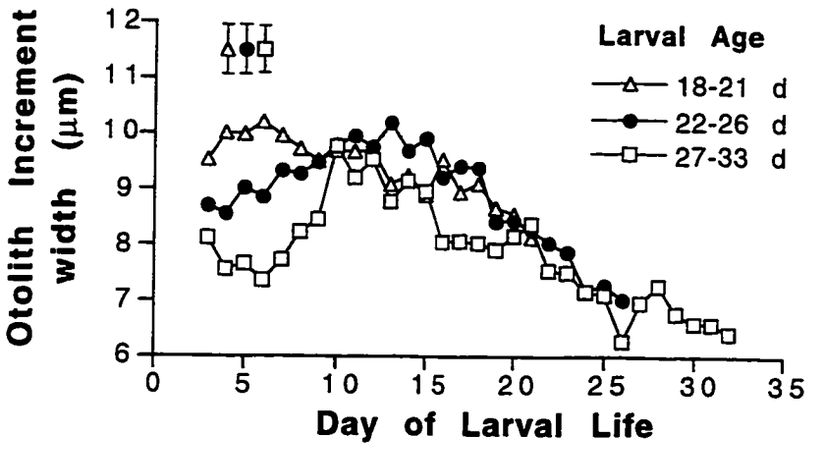

Figure 3b. Lapilla increment widths of *S. partitus* recruits with short (18-21 d, n=20), average (22-26 d, n=36) and long (27-33 d, n=13) larval durations. Range of average age larvae are those fish within approximately 1 standard deviation of the mean age (23.8 d ± 2.68). 95% CI of the mean shown in upper left.

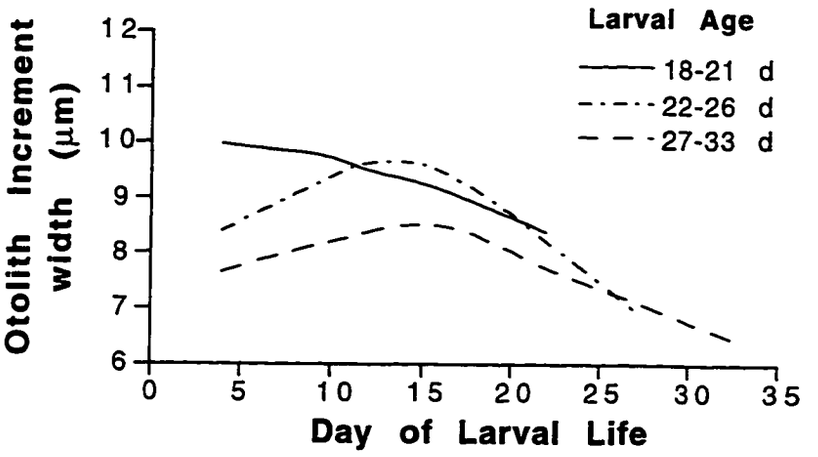

Figure 3c. Weighted averages (50%) from Figure 3b showing general trends in lapilla increment widths of young (18-21 d, n=20), average (22-26 d, n=36) and old (27-33 d, n=13) *S. partitus* larvae.

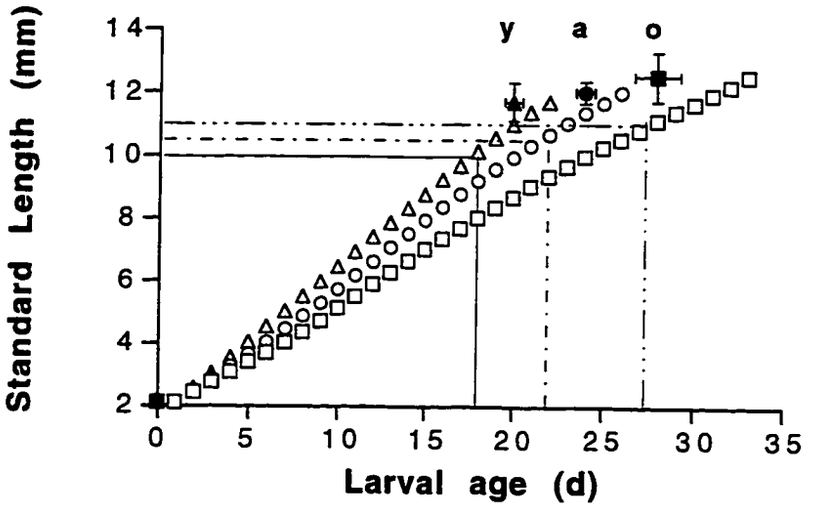

Figure 4. Larval growth trajectories calculated from lapilla otolith increments for young (y), average (a) and old (o) larvae. Horizontal lines indicate the smallest larvae collected from each age class (y=10 mm, a=10.5 mm, o=11 mm). Vertical lines represent the corresponding ages within each age class. These ages coincide with their lower limits (y=18 d, a=22 d, o=27 d). Corresponding filled symbols indicate mean (± 95% CI) size and age at settlement.

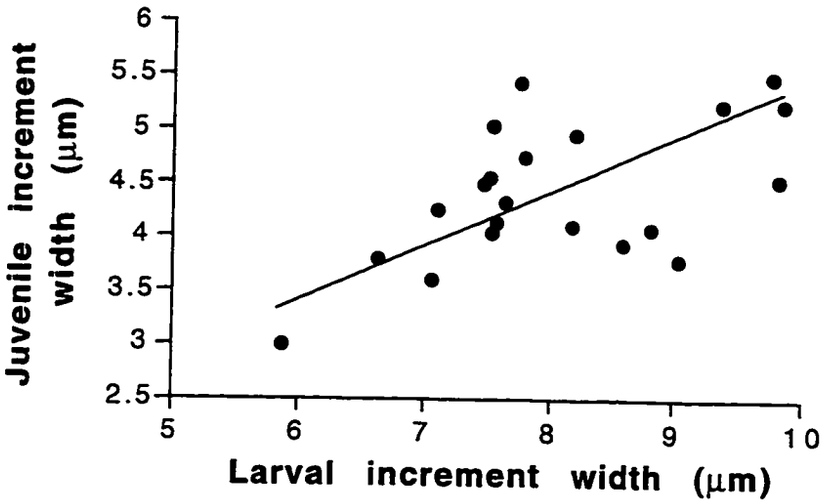

Figure 5. Relationship between late larval and early juvenile growth rates. Values are the average otolith increment width of the last 5 days presettlement (larval) and the average of the first 10 days postsettlement (juvenile) for 22 fish. Line fitted with regression analysis, $y = 2.515 + 0.397x$, $r^2 = 0.42$, $p<0.001$.

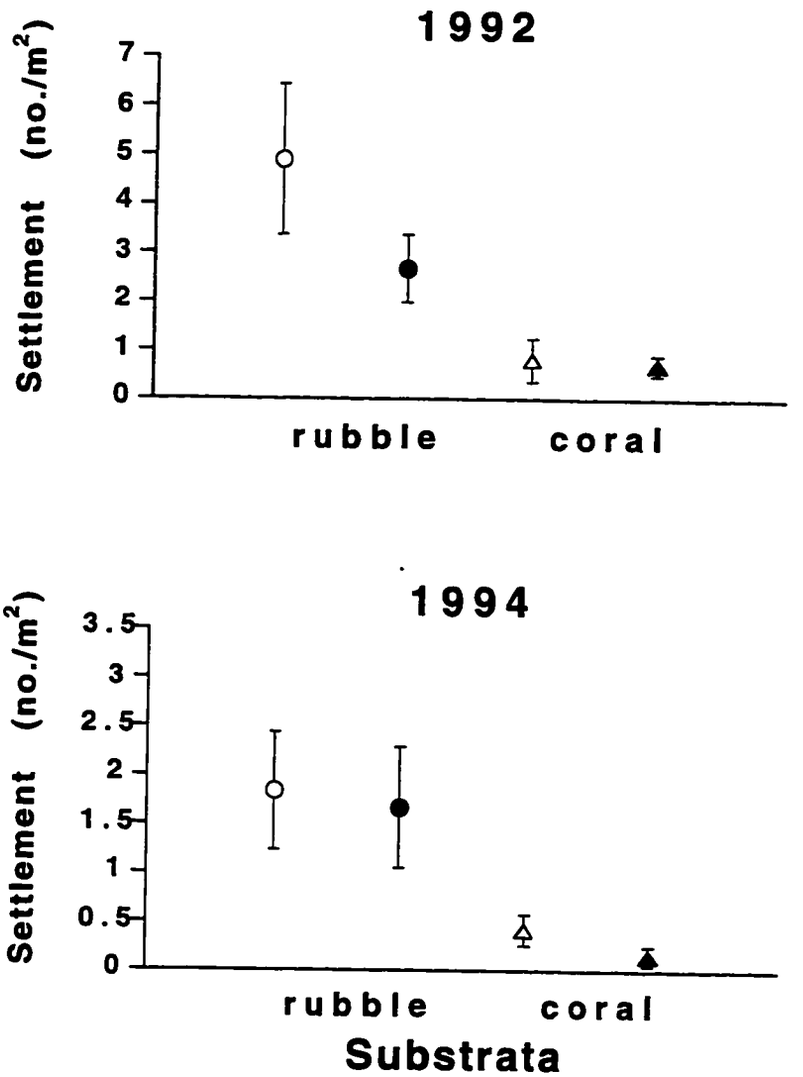

Figure 6. Daily settlement patterns of *S. partitus* during summer of 1992 and 1994 showing the mean density of larvae (±1 s.e.) arriving to the six replicates of each treatment. Substrata type (circles = dead *P. porites* rubble, triangles = live *M. annularus* coral colonies) and presence of conspecific adults (open symbols = adults absent, filled symbols = adults present).

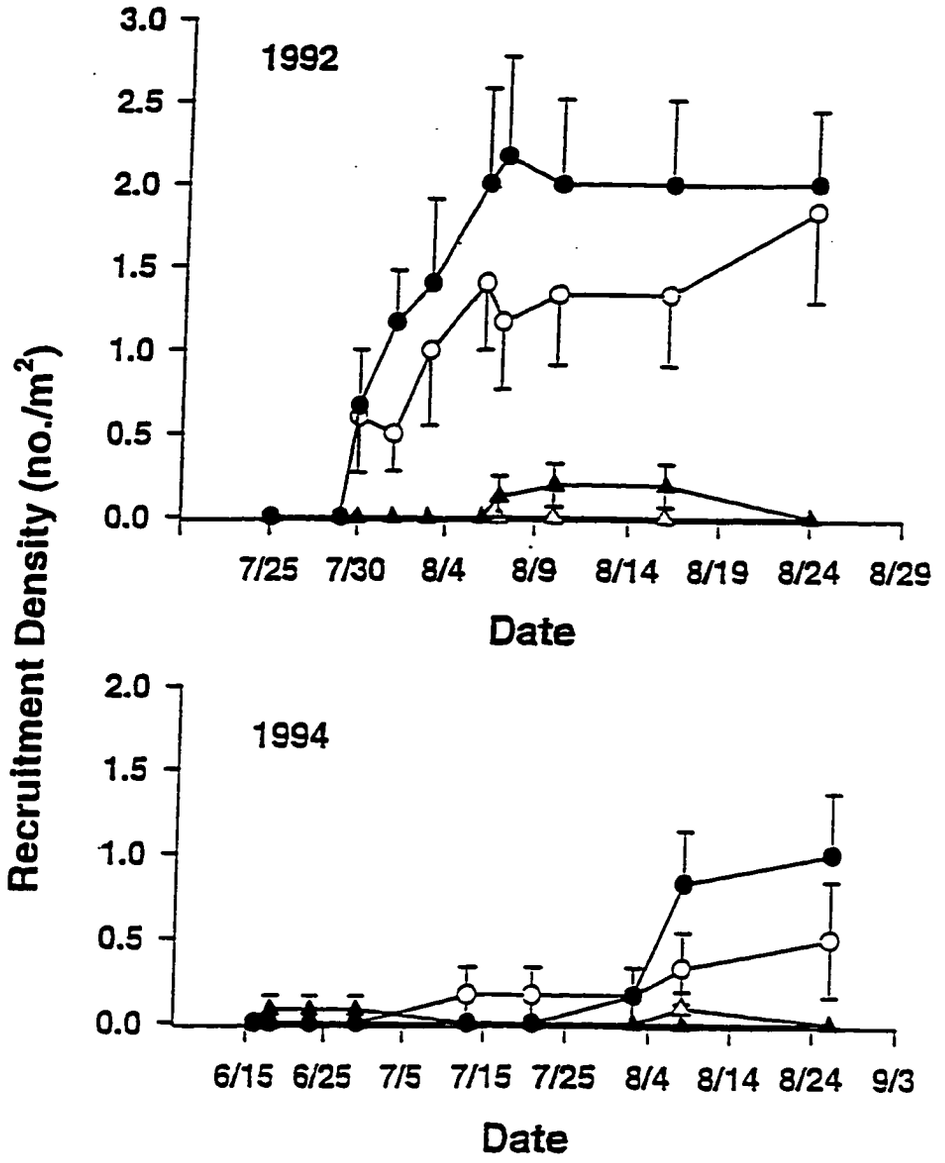

Figure 7. Persistence of newly recruited *S. partitus* over time during summer of 1992 and 1994. Each symbol represents the mean (±1 SE) density of juveniles censused on the six replicates of each treatment. Only days where all experimental units were censused are included. See Figure 2 for symbol legends.

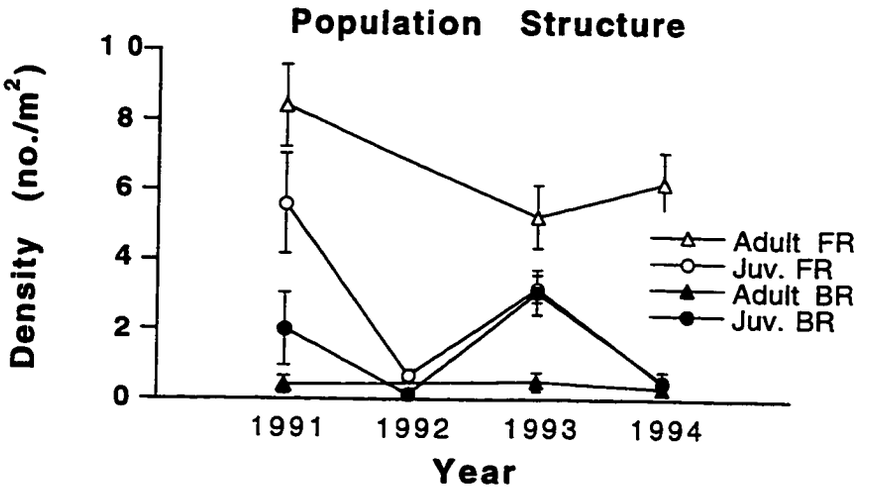

Figure 8. Mean density (±1 SE) of *S. partitus* juveniles (<25 mm SL, circles) and adults (triangles) in back reef (BR) and fore reef (FR) for July, 1991 to 1994. No data available for adult densities in 1992. Densities are for 30 m^2 strip transects.

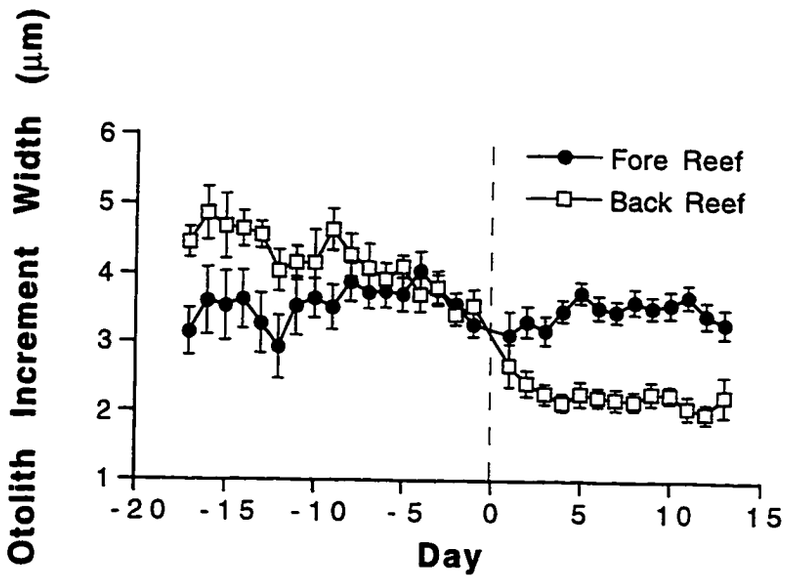

Figure 9. Growth rates (+1 SE), based on otolith increment widths, of juvenile bicolor damselfish. Dashed vertical line (day = 0) indicates date of capture and experimental manipulation of wild fish caught on the Teague Bay reef. Tagged fish (n=32) were randomly selected and transplanted to isolated coral heads and rubble piles on the fore reef (●) or back reef ( ) and recaptured 13 d later. Left side of vertical line (negative days) shows natural variation in growth rates of both groups in the days before capture.

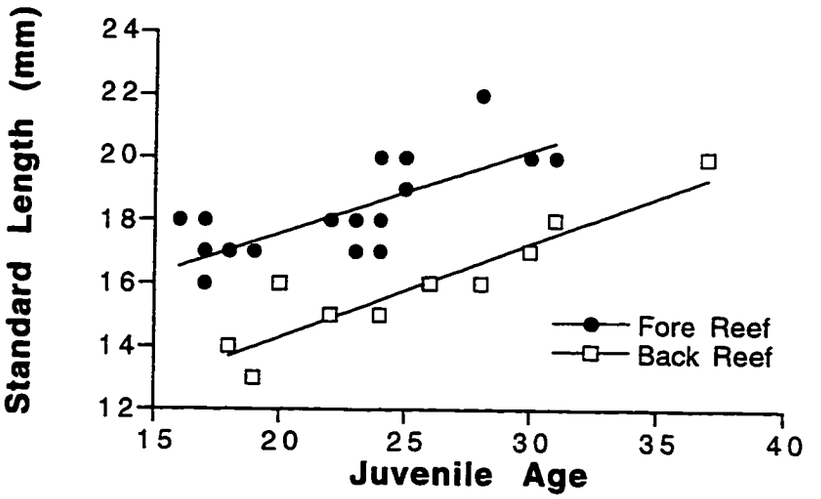

Figure 10. Relationship between standard length (mm) and age (d) of juvenile *S. partitus* recaptured from fore reef (●) and back reef ( ). Slopes of lines are homogeneous ($F_{1,31}$ = 0.247, p=0.623) regression equations but line intercepts are significantly different ($F_{1,31}$ = 81.348, p<0.001). fitted with for fore reef (sl = 12.262 + 0.265(age), r2 = 0.63, p<0.001) and back reef (sl = 8.362 + 0.297(age), r2 = 0.86, p<0.001).

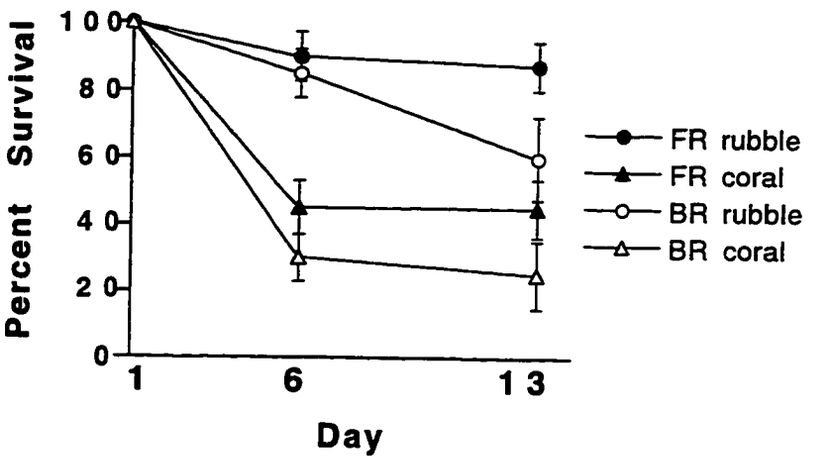

Figure 11. Percent survival (+1 SE) of juvenile *S. partitus* over a 13 d period. Fish were living on either *P. porites* rubble or *M. annularis* coral substrates in fore reef (FR) or back reef (BR) habitats. All experimental units received densities of four fish/m^2 on day 1. ANOVA showed a significant effect of substrata type ($F_{1,12} = 16.44$, $P = 0.002$) and reef zone ($F_{1,12} = 10.46$, $P = 0.007$). Interaction term was not significant ($F_{1,12} = 1.48$, $P = 0.248$).

CHAPTER II

THE EFFECT OF NATURAL VARIATION IN SUBSTRATE ARCHITECTURE ON THE SURVIVAL OF JUVENILE BICOLOR DAMSELFISH

SUMMARY

Coral reefs offer settling fish larvae a spatial mosaic of substrata that differ not only in structural complexity but also in the abundance and diversity of predators. This study provides direct empirical evidence that the interactions between predators and prey are causally linked to the variation in relevant architectural characteristics of natural substrates. Juvenile bicolor damselfish (*Stegastes partitus*) recruiting to the live boulder coral, *Montastrea annularis* experienced greater mortality than fish recruiting to rubble of dead *Porites porites* coral. Architectural differences, variable encounter rates with predators, and access to different food sources all contributed to higher mortality. Spatial (the number and size of suitable shelters) and structural (the arrangement of accessible crevices) differences among refuges provided by the two substrates were most important in affecting survival. *Porites* rubble contained almost three times the number of crevices than did *Montastrea* coral (39.9 vs. 14.3 crevices/m^2), had a much smaller mean crevice size than *Montastrea* coral (15.9 vs. 48.5 cm^2), and had a more complex

internal structure. In contrast, *M. annularis* has limited small crevices interspersed among numerous large holes which can shelter piscivorous predators. Survival of juvenile fish living on *Montastrea* coral was more strongly correlated to increases in crevice density (r^2=0.41) whereas survival of fish living on *Porites* rubble was more strongly correlated to crevice size (r^2=0.43). The effect of these natural differences in architecture on the mortality schedule of juvenile *S. partitus* was experimentally tested in the field using a combination of natural and artificial substrates. By varying the number of large shelters (adding PVC tubes) while controlling for the amount of small shelters (using natural rubble), it was found that the survival rates of juvenile bicolor damselfish varied inversely with the number of large shelters whereas the density of potential predators visiting the experimental units increased directly with the number of large shelters.

INTRODUCTION

Defining the factors and processes that produce the patterns of distribution and abundance of a species across a region has been of primary interest to ecologists for decades. Andrewartha and Birch (1954) considered that one of the most fundamental behavioral patterns of all organisms is the selection of a special place to live. In marine organisms with dispersive planktonic larvae the process of selecting an appropriate habitat begins at settlement, when invertebrate and fish larvae enter the structurally complex benthic environment. For a population to persist, each individual must locate habitat suitable for providing sufficient food for growth and reproduction and sufficient shelter for minimizing the risk of predation and

other environmental hazards. Unless constrained by some life history trait or other condition (e.g. small size, limited mobility, or isolation from other favorable habitats) many organisms can behaviorally modify their risk of predation by moving into habitats providing greater protection (Helfman 1986; Lima and Dill 1990; Eggleston and Lipcius 1992; Sweitzer and Berger 1992). Prey living in habitats of greater structural complexity typically experience decreased risk of predation from their natural enemies (Werner et al. 1983; Herrnkind and Butler 1986; Hacker and Steneck 1990; Sweitzer and Berger 1992; Eggleston and Armstrong 1995). This paper addresses the importance of spatial and structural differences among natural substrates in determining the mortality schedules of a coral reef fish.

The structural complexity of a habitat can be a useful predictor of the abundance, distribution and diversity of assemblages of birds (MacArthur and MacArthur 1961), lizards (Pianka 1966), marine fishes (Risk 1972; Luckhurst and Luckhurst 1978; Gladfelter et al. 1980; Bell and Galzin 1984; Sale 1984; Sale et al. 1984; Roberts and Ormond 1987; Levin 1991; Booth and Beretta 1994; McCormick 1994) and marine and aquatic invertebrates (Nelson 1979; Edgar 1983; Leber 1985; O'Conner 1991; Schneider and Mann 1991). The interacting effects between predation pressure and structural complexity determine the behavior, distribution and mortality rates of different species (Eklov and Persson 1996). Experimentally manipulating different types of natural or artificial substrates can help to identify the important structural traits that favor survival (see summary by Gotceitas 1989; review by Heck and Crowder 1991). The majority of these field and laboratory studies, using macro invertebrates as the prey, have documented a positive correlation between survival and degree of structural complexity (Hacker and Steneck 1990 and references therein).

Although it has been known for nearly two decades that mortality rates of newly settled reef fish are species-specific and show considerable spatial and temporal variation (Demartini and Anderson 1980; Jones 1984, 1986; Eckert 1985; Aldenhoven 1986; Sale and Ferrell 1988), the relationship of structural complexity to survivorship of reef fishes is not well understood (but see Jones 1988; Connell and Jones 1991). The typical method of measuring structural complexity of the reef has been to use the ratio of the length of a chain contoured over the substrate to the length of the same chain pulled taut (Risk 1972; Luckhurst and Luckhurst 1978; although see McCormick 1994). A ratio of 1.0 indicates a flat surface while larger values indicate greater structural complexity. Although the chain method provides a measure of vertical relief or rugosity it does not define whether large substrate complexity values are the result of many small crevices or few large crevices. The size and number of crevices are attributes of habitat complexity often overlooked but are likely to reduce the efficiency of predators. The relationship of animal body size to shelter size and the number of accessible shelters are critically linked to avoidance of predation (Shulman 1984; Roberts and Ormond 1987; Steger 1987; Moran and Reaka 1988; Hixon and Beets 1989, 1993; Eggleston and Lipcius 1992). The Limited Shelter Hypothesis was proposed as a general mechanism in structuring reef-fish communities (Randall 1963; Sale 1977, 1978; Smith 1978; Hixon and Beets 1989). This hypothesis states that "structural shelter of the appropriate size is a primary limiting resource for reef fishes" (Hixon and Beets 1989).

The purpose of this study was to document the spatial and structural characteristics of two common natural substrates found on coral reefs in the Caribbean, and to determine their effect upon survival rates of juvenile bicolor damselfish (*Stegastes partitus*). Natural variation in architecture of

live *Montastrea annularis* coral and dead *Porites porites* coral rubble was correlated with differences in survival and feeding behavior, and frequency of occupation by potential predators. Differences in substrate architecture were experimentally tested by manipulating size and frequency of shelters using a combination of natural and artificial substrates. These manipulations had a direct effect upon mortality schedules.

MATERIALS AND METHODS

Study Species

Damselfishes (Pomacentridae) are well known for their strong site fidelity where individuals defend a territory from settlement through adulthood (Sale 1980). The bicolor damselfish (*Stegastes partitus*) is a common fish on Caribbean coral reefs. It typically recruits to rubble substrates composed of dead *Porites porites*, *Acropora cervicornis* and *A. palmata* corals, to live *Montastrea annularis* boulder corals, and to a variety of low lying corals and sponges surrounded by sand (Emery 1968, 1973). *S. partitus* recruits are often extremely abundant on the rubble mounds constructed by the sand tilefish (*Malacanthus plumieri*). *Porites porites* rubble and *M. annularis* colonies are both abundant and ubiquitous substrates in the Caribbean but they differ in their architecture. *S. partitus* feeds on benthic invertebrates and algae as early juveniles becoming predominately planktivorous with age (Emery 1968, 1973). Greatest population densities tend to occur in areas of high current flow (presumably areas of good plankton supply) as on the

buttress of fringing reefs but also on the reef slope and reef base of barrier reefs (Emery 1968, 1973; Stevenson 1972; Nemeth pers. obs.) .

Experimental Procedure

The natural variation in structural characteristics of two common substrates was measured to determine if it contributed to differences in juvenile bicolor damselfish mortality rates. A total of 32 isolated *Montastrea annularis* coral heads were selected, and 32 *Porites porites* rubble piles (1 m^2) were constructed in 1993. Half of the experimental units were located on the fore reef and half on the back reef of Teague Bay, St. Croix, USVI. The rubble piles were meant to mimic the natural rubble mounds of the sand tilefish and were built by collecting rubble from the surrounding reef and depositing it in piles on barren sand. *Montastrea* coral heads averaged 2.09 m^2 (±1.33 s.d., range = 1.08 to 2.94 m^2) in area and 0.74 m (±0.159 s.d.) in height. The number and size of crevices were used to quantify differences in substrate architecture on coral and rubble. These attributes were measured by stretching two transect tapes over the two longest perpendicular axes of *M. annularis* coral heads and rubble piles constructed of dead *P. porites* coral. The length and width of all holes that were greater than 1 cm deep, and were crossed by the tape, were counted and measured with a plastic ruler to ±1 mm.

Quantitative data included mean crevice size (cm^2), mean crevice density (#/m^2), and the cumulative frequency of crevices <50 cm^2 and >50 cm^2 in area. Selected crevice size intervals (<25 cm^2, 26 to 50 cm^2, 50 to 149 cm^2, and >150 cm^2), mean crevice density and mean crevice size data were compared between substrate types with one-way analyses of variance. Selected crevice size intervals were roughly comparable to the small and large

crevices (24 cm^2 and 168 cm^2) used by Hixon and Beets (1993). Preliminary analysis of substrate architecture indicated that for both *M. annularis* coral heads and *Porites* rubble piles there were no differences in the average crevice number ($F_{1,60}$=0.788, P=0.378) or average crevice area ($F_{1,60}$=0.715, P=0.401) between fore reef and back reef zones. Therefore, data from back and fore reef habitats were combined before analysis of the effects of substrate characteristics on fish survival.

The experimental units examined above were part of a larger experiment where juvenile bicolor damselfish were stocked at 4 fish/ m^2 on both substrate types (Chap. 3). Survival of juvenile bicolor damselfish was estimated during periodic censuses of the experimental units. Since survival was partly affected by habitat (fore reef vs. back reef, Chap. 3) a one-way ANOVA was used to compare survival among substrate types (coral head vs. rubble pile) only on the fore reef. The proportion of fish surviving was transformed with an arcsin square root transformation (Zar 1984) prior to analysis. Single linear regression was used to examine how structural architecture (mean crevice density and mean crevice area) correlated with juvenile survival.

Feeding behavior was recorded for three juvenile *S. partitus* on each experimental unit. These data included feeding rate in planktonic vs. benthic foraging habitats, percent time spent feeding in each habitat and the maximum height fish attained while feeding above substrate. I estimated height using a scale bar attached to a dive slate. Since feeding behavior was correlated to observation date and not all fish or fish on all experimental units were watched during a single date, each fish was considered a single datum point. Thus feeding behavior and height above substratum were analyzed with a one-way analysis of variance with substrate type (coral vs.

rubble) as a fixed factor. Date was included in model since planktonic feeding rates tracked plankton food supply (Nemeth in prep).

In 1993 potential predators occupying the experimental units were counted only once. To gain a more accurate picture of predator use of *Montastrea* coral and *Porites* rubble, predators were counted five more times the following summer (1994) on 24 coral heads and 24 rubble piles including the 16 coral and 16 rubble fore reef experimental units used in 1993. Criteria for identifying potential predators were based upon Randall's (1967) gut content analysis of Caribbean reef fishes. All species that had greater than 20% gut volume represented by fish were considered potential predators and included groupers (Serranidae: *Epinephelus guttatus, E. adscensionis, Cephalopholis cruentata, C. fulvis*), lizardfish (Synodontidae: *Synodus intermedius*), trumpetfish (Aulostomidae: *Aulostomus maculatus*), moray eels (Muraenidae: *Gymnothorax moringa, G. miliaris, G. funebris*), scorpionfish (Scorpaenidae: *Scorpaena plumeri*), hamlets (Serranidae: *Hypoplectrus* spp.), and snappers (Lutjanidae: *Lutjanus apodus, L. mahogoni, Ocyurus chrysurus*). Since the number of predators on each experimental unit was typically 0 or 1, occasionally 2 and rarely 3 or 4, the counts were compared between substrate types using a 2 X 2 contingency table with substrate (coral or rubble) as the independent variable and presence or absence of predators as the dependent variable.

The above analyses of shelter characteristics, primarily the differences in size and frequency of crevices among *M. annularis* coral heads and *P. porites* rubble piles, illuminated the need for an experiment to isolate the effects of large and small shelters on damselfish survival. In particular, did the relative abundance of large shelters on *M. annularis* coral heads contribute to juvenile mortality? I tested this hypothesis by manipulating the number of

large shelters using artificial substrates while holding the number of small numerous shelters relatively constant. The artificial substrates (Itzkowitz 1990) consisted of 4 sections of PVC pipe 10 cm long with a 7.5 cm inside diameter (45 cm^2 hole). The pipes were secured to a plexiglass base to form a cross (Fig. 1A). Thirty artificial substrates were placed in a large sand channel (water depth 11-15 m) on the fore reef of Discovery Bay, Jamaica. Each artificial substrate was at least 3 m from other artificial substrates and from the reef buttress. *Porites* rubble was piled on top of the artificial substrates to provide shelter for juvenile damselfish (Fig. 1B). The number of large shelters were varied by filling either 0, 2 or 4 holes with rubble, giving 10 replicates of each treatment.

Juvenile bicolor damselfish (10-20 mm SL) were collected from surrounding area, tattooed to distinguish them from naturally recruiting fish and held in aquaria for 24 hr. Seven fish were released on each experimental unit on 25 January, 1995. At release, fish were observed for several minutes to verify that they remained on reef. Bicolor damselfish, potential predators, and all other fish, resident or visiting the units, were counted on days 1, 4 and 6. Since many of the experimental units had three or fewer bicolor damselfish present by day 6, the experiment was repeated on 1 February by returning the density of tattooed juvenile bicolor damselfish to 7 fish/unit. All fish were again counted on days 4, 10, 15, 18 and 21 when the experiment was concluded. Data were analyzed using a repeated measures analysis of variance test with hole number (0, 2 or 4) as the independent variable (3 levels) and number of fish surviving as the dependent variable. Similar to the experiment in St. Croix, the number of predators on each experimental unit was typically 0 or 1 and occasionally 2. Thus, predator counts were organized and analyzed using a 2 X 3 contingency table with treatment (0, 2

and 4 holes) as the independent variable and presence or absence of predators as the dependent variable.

RESULTS

Natural Variation in Substrate Characteristics

A significantly greater percentage of juvenile bicolor damselfish survived on *Porites* rubble than on *Montastrea* coral (80.51% vs. 70.11%, $F_{1, 30} = 5.601$, $P < 0.02$). Analysis of substrate architecture indicated that *Porites* rubble had a greater number of smaller crevices (<50 cm^2) than *Montastrea annularis* coral (Fig. 2A). Moreover, average crevice size was three times smaller on rubble piles than on coral heads (Table 1A). In contrast, *M. annularis* coral had a greater range and number of large crevices (>150 cm^2) relative to rubble (Fig. 2B, Table 1B). The mortality response of juvenile S. *partitus* to the two architectural characteristics (mean crevice size and density) was similar among both substrate types but the primary significant effect was surprisingly different. The regression analysis indicated that survival was positively correlated with the number of crevices but negatively correlated with the size of crevices on both substrate types (Fig. 3, 4). Interestingly, crevice density had a greater effect on fish survival on *Montastrea* coral (Fig. 3A) whereas average crevice size had a greater effect on fish survival on *Porites* rubble (Fig. 4B).

Feeding behaviors of fish living on each substrate type were different. Planktonic feeding rate (bites/min ± st. err.) of juvenile *S. partitus* was significantly higher ($F_{1,102} = 3.956$, $P < 0.05$) for fish living on coral heads (9.16

± 0.529, n = 51) than for fish living on rubble (7.63 ± 0.555, n = 53). However, no difference in benthic feeding rates were detected ($F_{1,102} = 0.091$, $P < 0.76$) among substrate types (coral 1.86 ± 0.244 vs. rubble 1.77 ± 0.170, n = 104). When feeding in the plankton, fish living on coral heads swam higher up into the water column and subsequently further away from shelter (Fig. 5). Analysis of predator counts found no detectable difference in the number of predators on coral heads and rubble piles (Chi-square = 0.961, d.f. = 1, P = 0.327).

Table 1. Summary of (A) average crevice size and (B) average crevice density at various crevice size (cm^2) intervals on *Porites porites* rubble piles and *Montastrea annularis* coral heads. Results of one-way ANOVA's comparing crevice size and crevice density intervals between *Porites* rubble and *Montastrea* coral.

A

	N	Crevice size cm^2 (±1 SD)	Range	$F_{(1,60)}$	P
Porites rubble	32	15.9 (4.26)	7.6-24.8	70.82	<0.001*
Montastrea coral	32	48.5 (21.27)	20.7-101.6		

B

Crevice size interval	Substrate	Crevice density #/m^2 (±1 SD)	Range (#/m^2)	$F_{(1,62)}$	P
≤25 cm^2	*Porites*	33.3 (6.26)	19-52	330.74	<0.001*
	Montastrea	8.9 (4.30)	3.1-20.3		
26 - 50 cm^2	*Porites*	3.8 (2.33)	0-9	11.17	<0.001*
	Montastrea	2.2 (1.31)	0.4-5.7		
50 - 149 cm^2	*Porites*	2.2 (1.48)	0-6	0.90	0.357
	Montastrea	1.8 (1.94)	0-10		
≥150 cm^2	*Porites*	0.6 (0.80)	0-3	19.31	<0.001*
	Montastrea	1.7 (1.20)	0-5.7		
Total crevices	*Porites*	39.5 (5.40)	25-53	294.05	<0.001*
	Montastrea	14.3 (6.27)	4.4-34.3		

* F ratios interpreted as significant.

Experimental Manipulation of Shelters

Mean crevice size on rubble piles was manipulated in a subsequent experiment in Jamaica using *Porites* rubble and artificial shelters with 0, 2 and 4 round holes (45 cm^2). The size of these holes was very similar to the average crevice size of *Montastrea* coral heads (48.5 cm^2). This experiment was designed to combine the attributes of *Porites* rubble (many small shelters) with the attributes of *M. annularis* coral (many large crevices), while controlling for variation in feeding behavior (same benthic food source, same access to plankton) of juvenile *S. partitus*. The repeated measures analysis of variance indicated that survival of *S. partitus* was significantly different among treatments (Table 2). Both trials of the experiment resulted in better survival on treatments with 0 and 2 large holes than on treatments with 4 large holes (Fig. 6).

Predation risk was measured as the presence or absence of predators seen on experimental units during each census. In Jamaica the number of piscivorous fishes observed occupying and visiting the artificial shelters increased with hole number (Fig. 7). There were significantly fewer predators counted on treatments with no large holes than on treatments with 2 or 4 large holes (Chi-square = 9.038, d.f. = 2, P = 0.011).

Table 2. Results of repeated measures ANOVA of survival of juvenile *S. partitus* among hole treatments (0, 2 or 4 large holes) during two trials of experiment in Discovery Bay, Jamaica. Duration of Trial #1 and #2 was 7 and 22 d, respectively.

Trial #1					
Among Treatments					
Source	**ss**	**df**	**ms**	**F**	**P**
Hole #	41.27	2	20.63	3.799	0.035*
Error	146.66	27	5.43		
Within Treatments					
Day	332.57	3	110.86	50.69	<0.001*
Day x Hole	16.73	6	2.79	1.28	0.278
Error	177.14	81	2.19		
Trial #2					
Among Treatments					
Source	**ss**	**df**	**ms**	**F**	**P**
Hole #	80.03	2	40.02	4.931	0.015*
Error	219.09	27	8.12		
Within Treatments					
Day	391.87	5	78.37	40.38	<0.001*
Day x Hole	17.50	10	1.75	0.90	0.534
Error	262.04	135	1.94		

* F ratios interpreted as significant.

DISCUSSION

The ability of prey to avoid being captured and eaten is related to their ability to detect and react to an approaching predator (Dill 1974). During an escape response, the time required to reach shelter will depend upon an individual's distance from shelter and its escape velocity (Dill 1990). Another component of a 'successful escape' is the degree of protection provided by that shelter. For a coral reef fish, a suitable refuge is a structure that provides the

necessary protection from a guild of local predators which vary greatly in their morphology and attack behavior. There is evidence that shelters close in size to the body size of the individual are most beneficial to survival (Randall 1963; Robertson 1979; Shulman 1984; Hixon and Beets 1989, 1993).

The suitability of crevices as refuges for juvenile bicolor damselfish (*Stegastes partitus*) was estimated by comparing several attributes of structural architecture among two common coral reef substrates, *Porites porites* rubble and *Montastrea annularis* coral. *Porites* rubble contained almost three times the number of crevices than *Montastrea* coral (39.9 vs. 14.3 crevices/m^2), had a much smaller mean crevice size than *Montastrea* coral (15.9 vs. 48.5 cm^2), and had a more complex internal structure (Fig. 5). Internal structure of rubble piles consists of a complex matrix of tunnels allowing multiple avenues of escape. In contrast, the surface of *M. annularis* colonies is typified by fist-sized knobs of living coral separated by shallow channels of dead coral. Only in some *M. annularis* coral heads does the columnar-lobate morphology (Weil and Knowlton 1994) form tunnels that descend deep into the center of the colony. These tunnels, however, are often occupied by moray eels (pers. obs.).

Juvenile *S. partitus* living on *Porites* rubble had greater survivorship relative to fish living on *Montastrea* coral. This same pattern was found in an earlier study where survivorship on coral averaged 44% while survival on rubble averaged 88% (Chap. 1). Consistent with the Limited Shelter Hypothesis (see Introduction), there was a positive effect of increasing crevice number and a negative effect of increasing crevice size on survival. However, these effects on survival were not expressed equally on both substrate types. The influence of crevice number on survival was more pronounced on *Montastrea* coral (Fig. 3A) whereas the influence of crevice

size on survival was more pronounced on *Porites* rubble (Fig. 4B). This result reflects the importance of substrate architecture in affecting the interactions between predator and prey (Eklov and Persson 1996).

As the number and size of large crevices is increased the distance between small crevices will also increase over the entire surface of a substrate. Moreover, these large crevices will be used sporadically by a variety of piscivorous fishes during their foraging forays. *Montastrea* coral heads had a significantly greater number of large crevices (Table 1, Fig. 2B) which simultaneously increases the distance between shelters suitable for a recruit, reduces the number of viable escape routes available to a recruit and potentially increases the number of lines of attack available to a predator.

The number of large shelters on a reef has been shown to have a positive effect on the number of predators and simultaneously have a negative effect on the number of prey (Hixon and Beets 1993). Based on this evidence it was expected that predator density would be higher on *Montastrea* coral due to the greater number of large crevices. However, the number of resident and visiting predators were not significantly different among the two substrate types. With predation intensity being equal among *Montastrea* coral and *Porites* rubble, the higher risk of predation on coral, due to its shelter characteristics, probably resulted in a higher rate of mortality. This conclusion is supported by the study conducted in Jamaica. In this experiment predators occupied 2-hole and 4-hole treatments at equal rates. Yet juvenile *S. partitus* survival rates were higher on reefs with 0 and 2 large holes than on reefs with 4 large holes. The contradiction in *S. partitus* mortality rates and predator occupation rates among 2-hole treatments may be explained by predator and prey behavior. Within the 4-hole rubble piles, a predator could attack a juvenile damselfish from any of four directions

because the PVC tubes formed a hollow cross (Fig. 1). On 2-hole treatments, however, half of each unit was relatively safe from ambush since two adjacent holes were completely blocked. Thus, if juvenile *S. partitus* concentrated their feeding efforts opposite the open tubes they could effectively eliminate the risk of being attacked even though predators were concealed within their rubble piles. On many occasions, juvenile *S. partitus* would swim to a large shelter and inspect a predator then resume feeding. These fish were apparently confirming the location of a predator and assessing its threat (Magurran et al. 1985; Pitcher 1992).

On natural substrates, the feeding behavior of an individual can influence its risk of predation. Juvenile *S. partitus* living on *Montastrea* coral heads foraged over three times higher relative to the top of the experimental units. Foraging height of planktivorous fishes is related to size of individuals, light intensity, availability of food and the presence of predators and competitors (Hiatt and Strasburg 1960; Stevenson 1972; Forrester 1991; Hobson 1991). Fish size and light intensity can be immediately eliminated as factors affecting foraging height in this study. Fish length did not differ among substrates and behavioral recordings alternated between coral heads and rubble piles within each observation date thus eliminating the bias of time of day. Fish living on coral heads spent a greater percent of their time feeding in the plankton indicating that benthic food (benthic algae, micro invertebrates) may have been less abundant on live coral heads relative to other substrates or that these individuals had greater access to planktonic organisms (Hobson 1991). Individuals competing for food would be inclined to swim further into the current giving them priority access to incoming plankton (Forrester 1991). *S. partitus* feeding height averaged 60 cm above the substrate for fish on coral, compared to 20 cm above the substrate for fish on

rubble. A 20 mm *S. partitus* living on a coral head would need to travel 20 body lengths further than a fish on a rubble pile given the 40 cm difference in average distance to shelter (Fig. 5). By venturing further from shelter, increased growth and reduced competition would come at the price of increased risk of predation (Dill and Houtman 1989; Dill 1990; Lima and Dill 1990). I observed a number of predation events on bicolor damselfish feeding in the plankton above a coral head. On one occasion a juvenile was attacked and eaten by a grouper (*Cephalopholis cruentata*) concealed within a large crevice of the same coral head. On another occasion a lizardfish (*Synodus intermedius*) from the sand attacked an adult bicolor damselfish feeding above its coral head. Feeding far from shelter to maximize energy intake highlights the trade-off between predation risk and loss of foraging opportunity (Dill and Fraser 1984).

Itzkowitz (1977) speculated that juvenile color patterns of three species of Caribbean damselfishes might function as cryptic coloration on specific substrates. For example, the yellow coloration of juvenile *S. planifrons* may be most cryptic on tan *M. annularis*, where they are commonly found (Tolimieri 1995). Juvenile *S. partitus* typically occur in sand/rubble habitats where their black and white coloration makes them less conspicuous. As an individual flees into a rubble crevice, the white posterior half of its body blends well with the sand/rubble substrate. As it peers out from its dark crevice its dark anterior half conceals it well. A second color variant with a yellow breast also commonly occurs on juveniles and adults which live on *M. annularis* coral (pers. obs.). The function of this color morph is unknown (Myrberg 1972; Emery 1973) but may be related to its diet or used to increase its crypsis. In this study, most individual *S. partitus* were the black and white variant, therefore differences in mortality of juvenile bicolor damselfish

placed on the two substrate types may have been a function of their coloration. Further experiments studying the function of juvenile coloration are needed.

The initial rates of mortality among the two trials of the experiment in Discovery Bay provide insight into the vulnerability of recruits under temporally variable environmental conditions. On 25 January, the start of the first trial, sea conditions were relatively rough (1-1.5 m swells) and large amounts of suspended sediments reduced underwater visibility. When released onto the rubble piles, most of the juvenile *S. partitus* had difficulty maintaining their position over the substrate due to the strong ground swell. Reduced visibility near the bottom probably helped conceal many predators as well. Initial predation was intense with some fish being eaten by the abundant graysby (*C. cruentata*) and coney (*C. fulvus*) residents in the PVC tubes. A few of the smaller recruits were even pursued by small serranids such as tobaccofish (*Serranus tabacarius*) and harlequin bass (*S. tigrinus*). The second trial of the shelter manipulation experiment commenced on a calm day with no initial mortality occurring. Subsequent mortality occurred at a much slower rate but resulted in the same outcome (Fig. 6). Many species of coral reef fishes have episodic settlement (Robertson et al. 1990) where arrival to the reef occurs a few days around the new moon. It is highly likely that if such a settlement pulse coincides with rough seas, post-settlement mortality may be unusually high.

Previous studies examining structural complexity have typically quantified gross reef morphology. Risk (1972), who measured substrate topographic complexity in St. John, USVI, found a positive correlation with fish species diversity but no relationship with total number of fish. Alternatively, Luckhurst and Luckhurst (1978), working in Bonaire and

Curacao, found positive correlation between rugosity and number of large fish species (>50 mm) but poor correlation with number of small fish species (<50 mm). Luckhurst and Luckhurst (1978) suggested that gross reef morphology is important for larger reef fish and individual substrate morphology and structure is important for small fishes (gobies and clinids). Measures of reef structure will need to incorporate different scales relevant to fish of different sizes. These might include gross reef morphology (rugosity index), individual substrate architecture (number and size of holes) and surface microtopography (Dahl 1973). This study provides direct empirical evidence that the interactions between predators and prey are causally linked to the variation in relevant architectural characteristics of natural substrates. Continued work on the relationships between prey species, their predators and the substrates they occupy is essential to making predictions of reef fish/habitat associations and the resultant mortality schedules encountered by different species within different habitats.

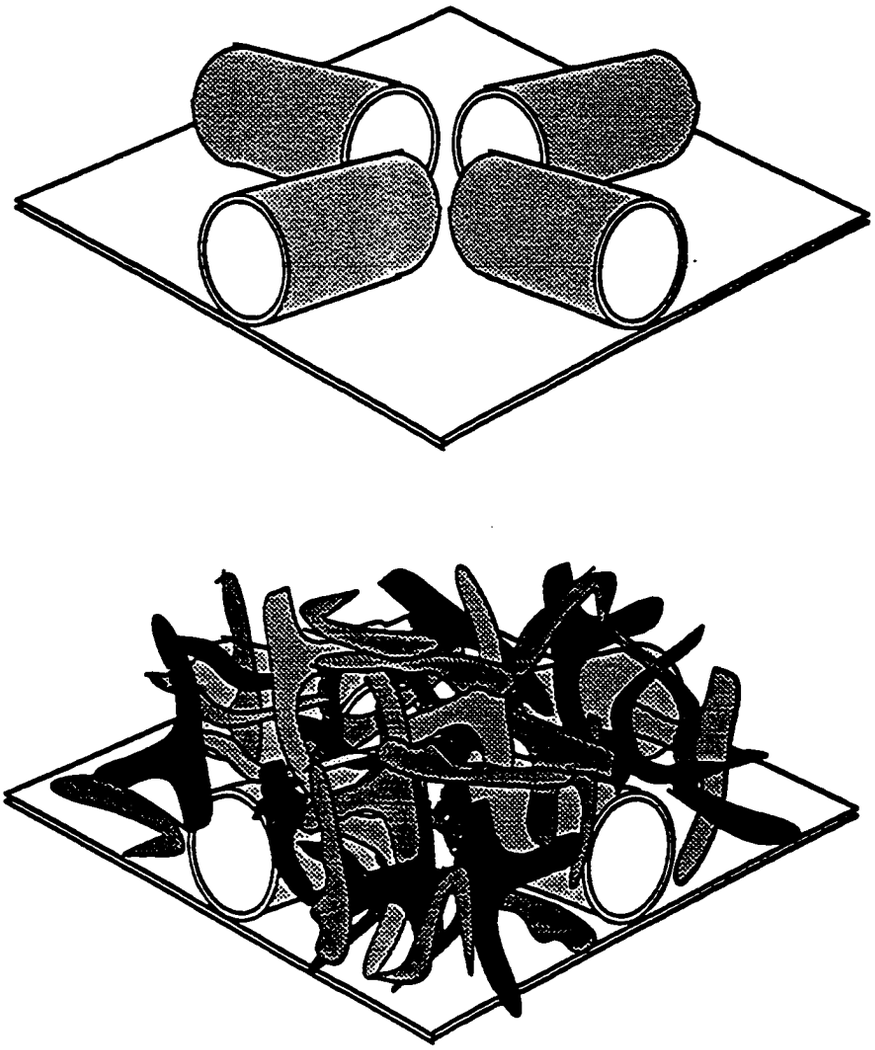

Figure 1. Diagram of artificial substrate (A) on top of which *Porites porites* rubble was piled (B). Rubble was used as shelter by juvenile bicolor damselfish. Large hole inside diameter is 7.5 cm (45 cm^2).

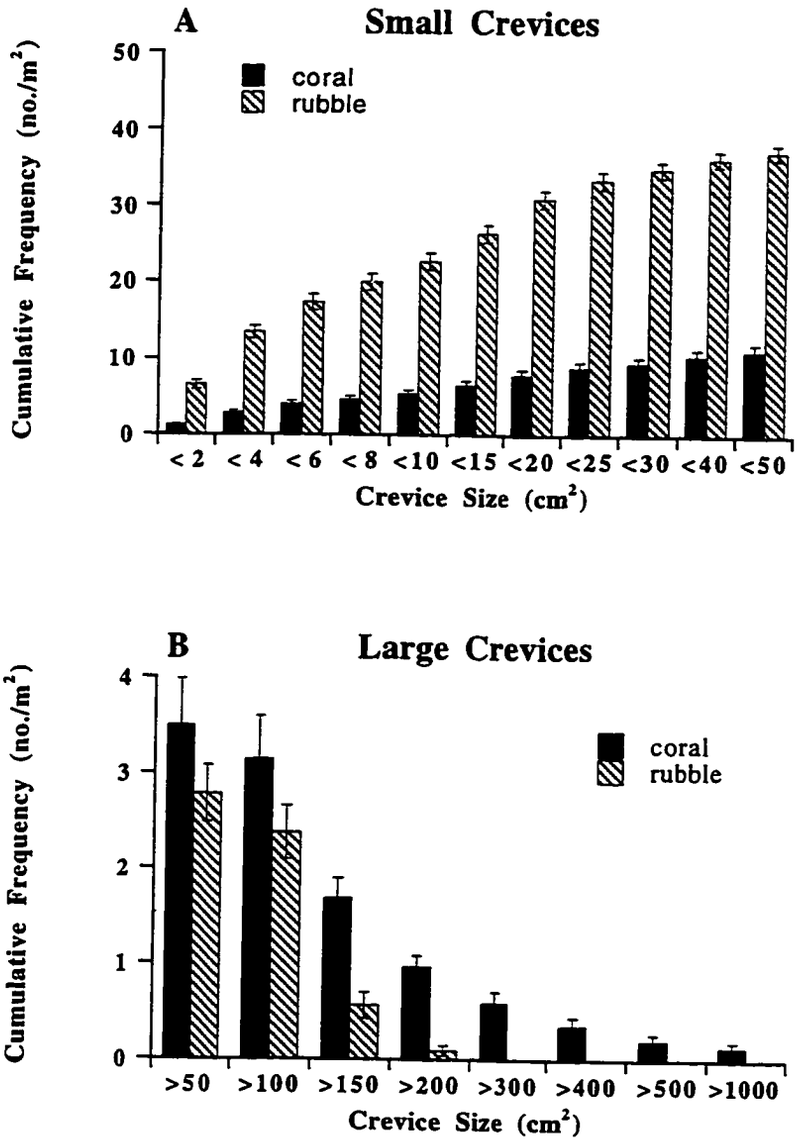

Figure 2. Mean cumulative frequency (± st. err) of A) small shelters from ≤2 cm^2 to ≤50 cm^2 and B) large shelters from ≥1000 cm^2 to ≥50 cm^2 (accumulates from large to small) on *Montastrea annularis* coral heads (n=32) and *Porites porites* rubble piles (n=32).

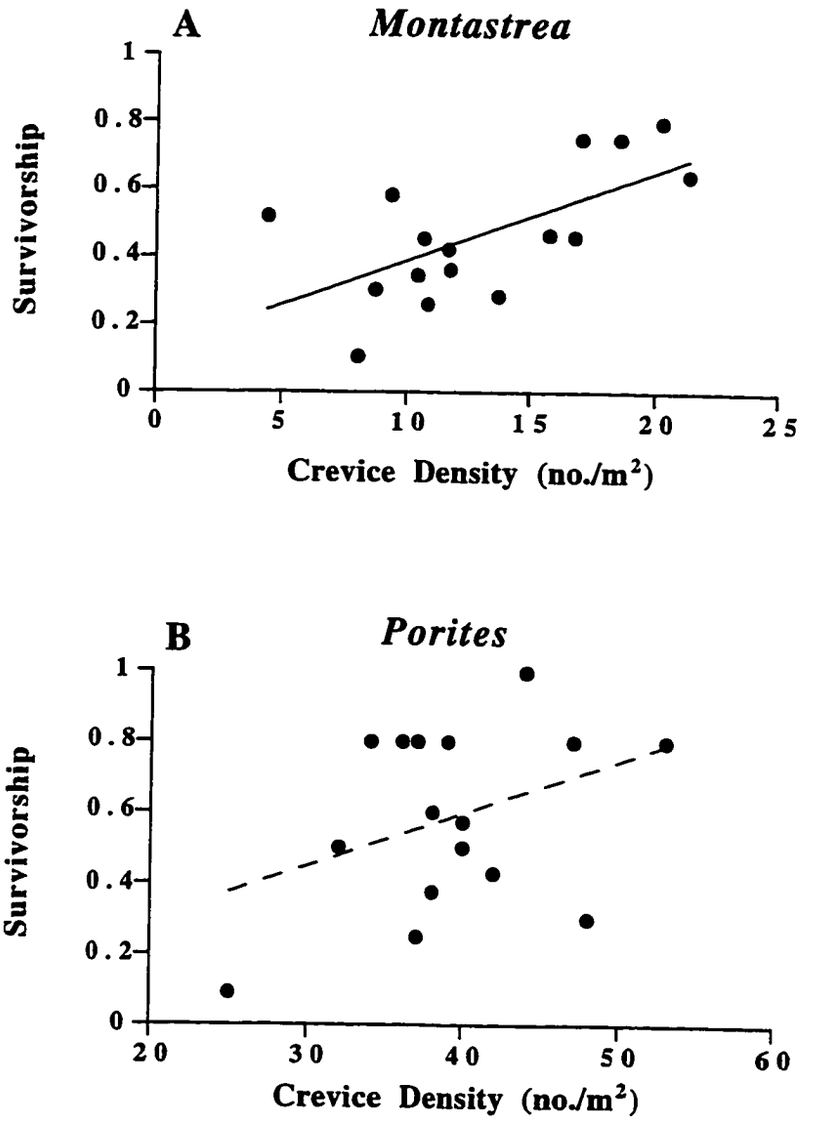

Figure 3. Regression plot of the proportion of juvenile bicolor damselfish surviving relative to the mean crevice density of each (A) *Montastrea* coral head ($y = 0.383 + 0.028x$, $R^2=0.41$, $F_{(1,14)}=9.648$, $P=0.008$), and each (B) *Porites* rubble pile ($y = 0.170 + 0.018x$, $R^2=0.16$, $F_{(1,14)}=2.746$, $P=0.12$). Note difference in scale of X axis.

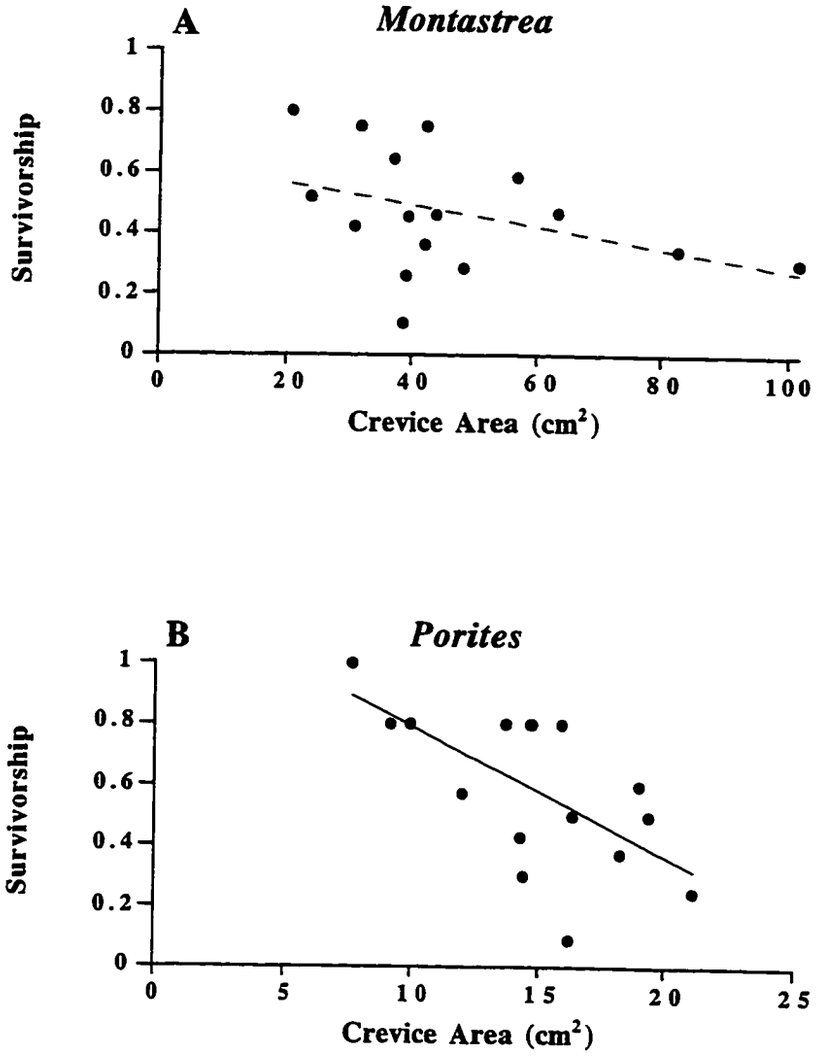

Figure 4. Regression plot of the proportion of juvenile bicolor damselfish surviving relative to the mean crevice area of each (A) *Montastrea* coral head ($y = 0.922 - 0.004x$, $R^2=0.13$, $F_{(1,14)}=2.165$, $P=0.163$), and each (B) *Porites* rubble pile ($y = 1.669 - 0.053x$, $R^2=0.43$, $F_{(1,14)}=2.746$, $P=0.006$). Note difference in scale of X axis.

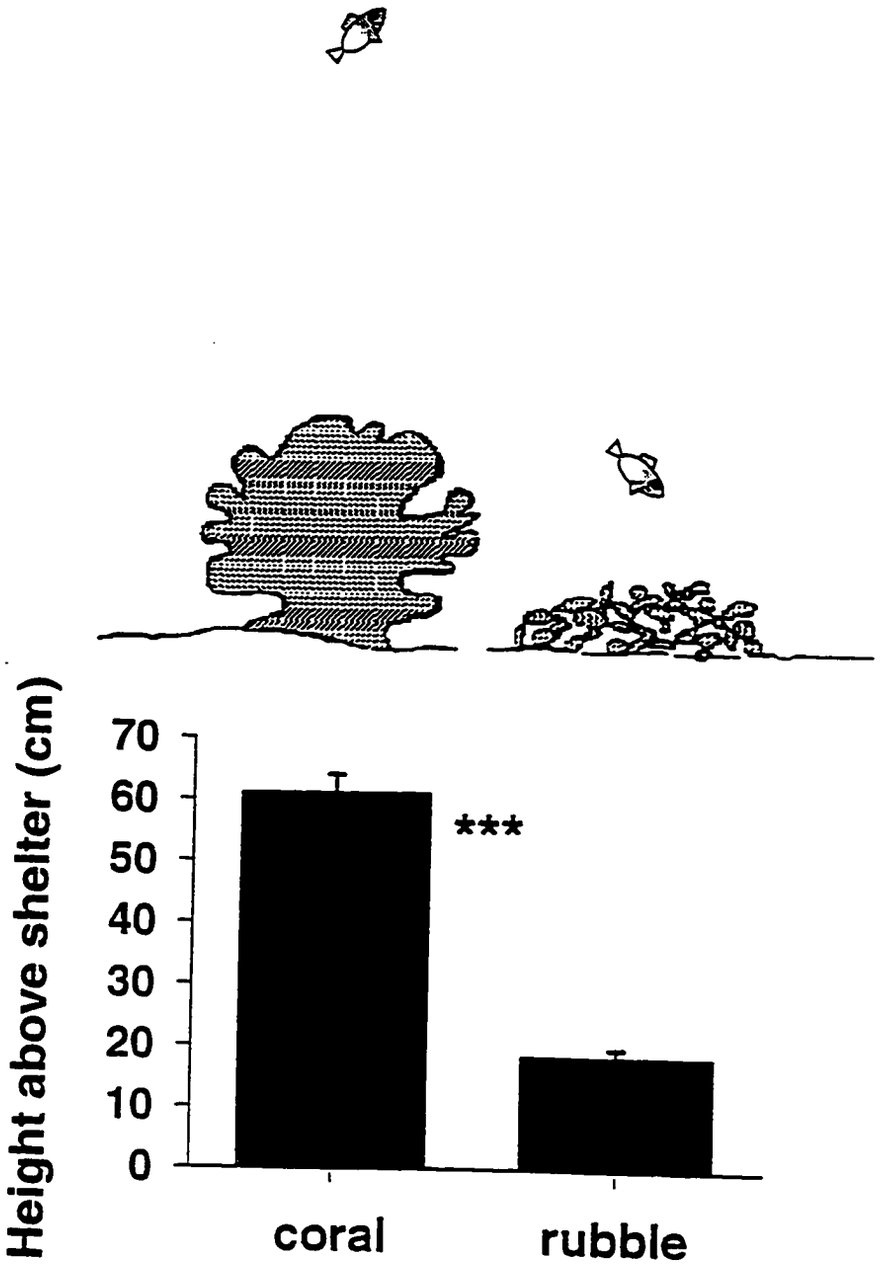

Figure 5. Diagram showing bicolor damselfish feeding in plankton from a *Montastrea annularis* coral head and *Porites porites* rubble pile. Both substrates are viewed in cross section to show external and internal structural architecture. Maximum height (cm) of fish above substratum is depicted as vertical bars (± standard error of mean, $^{***}F_{(1,14)}=73.84$, $P<0.0001$).

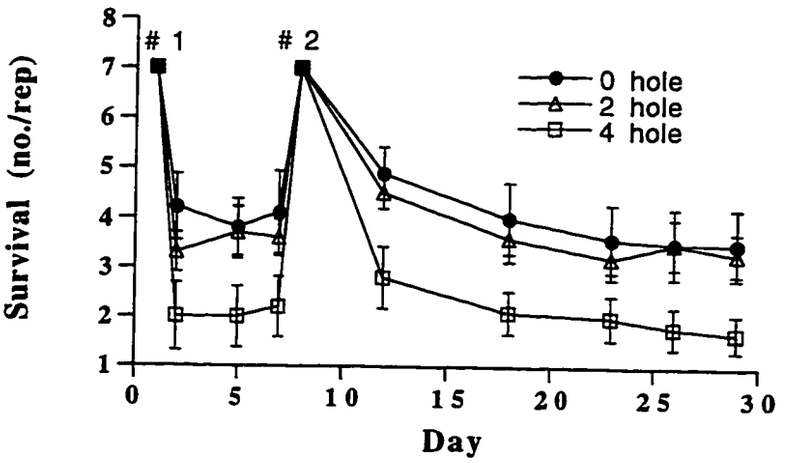

Figure 6. Survival rates of juvenile bicolor damselfish (mean no. fish ± s.e.) on experimental reefs containing either 0, 2 or 4 large (45 cm^2) holes. Study duration was 29 d where #1 and #2 indicate start date of two trials which had initial densities of 7 fish/unit. There were 10 replicates per treatment.

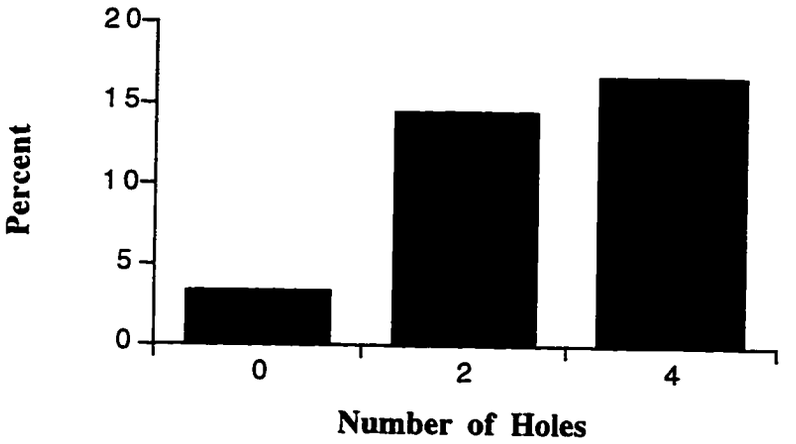

Figure 7. Percent of experimental reefs occupied by piscivorous predators during 29 d experiment. Reefs contained either 0, 2 or 4 large (45 cm^2) holes. There were 10 replicates per treatment.

CHAPTER III

THE CUMULATIVE AFFECTS OF PHYSICAL AND BIOLOGICAL FACTORS ON BICOLOR DAMSELFISH POPULATIONS

SUMMARY

Pomacentrids are well known to display distinct patterns of zonation within and among reef habitats throughout the Caribbean. The bicolor damselfish (*Stegastes partitus*) was used as a model species to examine the factors and processes responsible for the distribution patterns of juveniles and adults at three spatial scales: among two common substrate types, among back (BR) and fore (FR) reef habitats and among two distant islands. Results of a multifactorial experiment conducted in Teague Bay, St. Croix and Discovery Bay, Jamaica indicated that differential survival among substrate types (*Porites porites* rubble piles > *Montastrea annularis* coral heads) directly determined the small-scale distribution patterns of juvenile *S. partitus*. Among habitats (BR vs. FR) the combined effects of elevated aggressive interactions with another territorial pomacentrid (*S. leucostictus*) and lower rates of food supply to back reef habitats reduced juvenile growth rates by 50% relative to those of fore reef fish. These effects were identical between the islands of St. Croix and Jamaica. In St. Croix juvenile growth rate indirectly affected rate of mortality. In Jamaica, however, greater predation pressure

eliminated the growth advantage found in St. Croix and directly accounted for variation in mortality rate. These results provide strong evidence to account for the similar patterns of distribution of juveniles and adults found at a number of locations in the Caribbean.

INTRODUCTION

In any large, diverse community there will be a few species represented by many individuals and many species represented by few individuals (Andrewartha and Birch 1954). As one moves along an environmental gradient or through different habitats the relative proportion of these species will fluctuate. The central questions of ecological research have concerned the factors and processes that limit a species' population. In general, the distribution and abundance of a species will depend upon the influx of individuals into different habitats, the intensity of predation and interspecific competition for critical resources within these habitats, and the physical and biological conditions which favor one species over another.

In the marine environment, most fishes and invertebrates have the ability to disperse as pelagic larvae over large distances to patchily distributed habitats. Early studies on marine fish and invertebrate populations have stimulated recent debate on the factors structuring marine benthic communities (Connell 1985; Underwood and Fairweather 1989). Alternative explanations have contrasted the importance of variation in the arrival of colonizing individuals (review by Doherty and Williams 1988, Doherty and Fowler 1994) with the effects of processes occurring after settlement such as competition (Smith and Tyler 1972; Ehrlich 1975; Gladfelter et al. 1980;

Forrester 1995; Robertson 1996) and predation (Talbot et al. 1978; Shulman 1985; Shulman and Ogden 1987; Hixon 1991).

It is unlikely that a single mechanism is responsible for population regulation and reef fish community structure considering the great spatial heterogeneity of coral reefs over a wide range of scales. One of the most striking features of coral reefs is the classic physiographic zonation where the wave-exposed reef crest separates the back reef lagoon from the outer reef slope (Done 1983). Different factors and processes can operate at different places and at different times, and the relative magnitude of their effects will differ for juveniles and adults of a species (Jones 1987). Most studies exploring patterns of distribution and abundance of coral reef fishes have been largely descriptive (visual census of populations) where distributions were correlated to resource levels, especially among larger spatial scales (100's of meters to 1000's of kilometers; review by Williams 1991). At smaller spatial scales, experimental studies indicate that habitat selection by settling fish is important in determining distribution patterns among different substrates and within and among reef zones (Eckert 1985, 1987; Aldenhoven 1986, Meekan 1988, review by Doherty 1991, review by Williams 1991, Milicich et al. 1992, Wellington 1992, Tolimieri 1995). Moreover, juvenile growth and mortality rates can be modified by various benthic processes (Thresher 1983, Jones 1984, 1986, 1987; Shulman 1984, 1985; Shulman and Ogden 1987, Robertson 1988, Forrester 1990) and these effects will, in turn, alter the age structure of local populations. The local processes acting at the level of the individual should be detectable at larger spatial scales if the relative magnitude of the effects is proportional at these larger scales.

Coral reef fishes have open populations and are interconnected at the metapopulation level through arrival of dispersive larvae (Sale 1991). Since

the typical feed-back mechanisms of population control do not function in open populations (Roughgarden and Iwasa 1986; Roughgarden et al. 1988), the local physical and biological attributes will have potentially more variable effects on local population structure. The "scaling up" of the effects of benthic processes from local population to metapopulation levels is feasible when consistent patterns in the population structure of a species occur among distant sites. These patterns may reflect spatial similarities in the physical and biological processes within comparable habitats (Hiatt and Strasburg 1960) and thus may be conducive to experimental testing. An example of species-habitat associations at the metapopulation level is found in a group of six ecologically similar Atlantic pomacentrids of the genus *Stegastes*. The juveniles and adults of these species display distinct patterns of habitat use throughout the Caribbean (Florida: Emery 1973, Bahamas: Clarke 1977, Jamaica: Itzkowitz 1977, Panama and Puerto Rico: Waldner and Robertson 1980). In general, the adults of at least three species of damselfishes (*S. planifrons*, *S. fuscus*, and *S. partitus*) tend to dominate primary habitats with little overlap. Juveniles of these species, however, are more broadly distributed across habitats. Two other species, which overlap with the above three, are largely restricted to back reef (*S. leucostictus*) and fore reef (*S. variabilis*) zones (Wellington 1992). *Stegastes diencaeus* shows little habitat specificity. Speculation as to the mechanisms generating these patterns include habitat selection at settlement, differential mortality after settlement, or differential competitive abilities among species or size-classes (Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980; Wellington 1992; Robertson 1996).

In this study I use the bicolor damselfish, *Stegastes partitus* Poey (Perciformes, Pomacentridae) as a model species to examine the relative

importance of various mechanisms in affecting juvenile demography and producing the observed patterns of distribution and abundance. Juveniles are distributed among live coral (*Montastrea annularis, Porites porites*) and small rubble substrates (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Adults are largely restricted to fore reef slope, fore reef base and deep reef habitats. Their territories are most commonly located on *P. porites* and *M. annularis* colonies, and among large rubble and sponges. *Stegastes partitus* larvae settle to both back reef and fore reef zones at similar densities (Chapter 1), therefore habitat selection at settlement is probably less important in structuring adult populations than other benthic processes. Behavioral observations and a transplant experiment conducted in 1992 (Chapter 1) identified potential benthic mechanisms which may account for the lack of adults in back reef habitats. A multifactorial experiment was designed to simultaneously test the effects of reef habitat, substrate type and interspecific competition on growth and survival. These experimental treatments were established to simulate the conditions juvenile bicolor damselfish experience after settlement. The demographic responses to these conditions were measured on two islands, St. Croix and Jamaica, to examine the generality of the results.

MATERIALS AND METHODS

Study Sites

The experiments described in this paper were conducted in the Caribbean Sea on the islands of St. Croix and Jamaica which are about 1200 km apart

(Fig. 1). Teague Bay is enclosed by a bank-barrier reef on the northeast coast of St. Croix (Fig. 2). The tidal exposed reef crest separates the shallow back reef lagoon (5 - 8 m deep) from the fore reef slope and fore reef base (10 - 15 m). The shallow back reef (1 - 5 m) and shallow fore reef slope (1 - 10 m) are composed primarily of dead *Acropora palmata*, large live and dead *Porites porites* colonies, massive *Montastrea annularis* coral heads and a variety of other head coral species. The back reef slope varies in width from 2 to 10 m and gives way to sand substrate. Within the lagoon, isolated patch reefs composed of live *M. annularis* colonies or dead colonies covered with macroalgae are scattered throughout. Between patch reefs are beds of *Thalassia testudinum* sea grass and the conical mounds of *Arenicola cristata* lugworms which inhabit fine sandy sediments. The fore reef slope (10 to 50 m wide) descends to the reef base where isolated coral heads and patch reefs are surrounded by sand (Fig. 3). Massive heads of *M. annularis* dominate the fore reef base along with sea fans, gorgonians and sponges. Fifty to 100 m seaward from the reef slope are expansive manatee grass beds (*Syringodium filiforme*). A more detailed description of Teague Bay can be found in Ogden (1972) and Adey (1975).

Discovery Bay, on the north shore of Jamaica, is partially enclosed by a barrier reef (Fig. 2). Small islands of dead coral rubble, created during hurricane Allen in 1980 (Woodley et al. 1981), dot the narrow reef crest. In the shallow back reef (1 - 5 m depth), live and dead colonies of *M. annularis* and *Siderastrea siderea* are interspersed with sand and *T. testudinum* grass beds. This shallow shelf quickly descends into the deep (50 m) central lagoon which is composed of soft, fine sediments. From the reef crest, the fore reef slopes gradually for 100 - 200 m. In shallow depths (<10 m) bare coral rubble or dense macroalgae (*Sargassum* spp.) have supplanted the historical stands

of *A. palmata*. The topography at 10 - 20 m depth consists of coral spurs separated by sand channels. At these depths large *M. annularis* colonies, bare rubble and macroalgae dominate. Beyond 20 m, coral buttresses of large plating corals (*Agaricia* spp.) and chutes of fine sediments descend steeply into the oceanic trench (Fig. 3). A more complete description of Discovery Bay can be read in Goreau (1959) and Goreau and Goreau (1973).

Experimental Procedure

During July and August 1993, a series of experiments were used to determine the effects of different habitats, substrates and levels of interspecific competition on growth and mortality of juvenile bicolor damselfish, *Stegastes partitus*. The complete experimental design included reef habitat (fore reef vs. back reef), site nested within habitat (east vs. west), substrate type (*Montastrea annularis* coral heads vs. *Porites* rubble piles) and interspecific competition (0 vs. 5 *S. leucostictus* /m^2) as main effects, with four replicates per treatment (Table 1). Experimental procedure included the selection of sixteen coral heads and construction of sixteen rubble piles on sand flats at two sites on the fore reef base (15 m depth) and at two sites on the back reef (2 m depth) in Teague Bay, St. Croix, U. S. V. I. The two sites along the fore reef and back reef were approximately 100 m apart and provided a measure of variability within each reef habitat. All experimental units (coral heads and rubble piles) were separated by at least 3 m of barren sand from all other reef structures. The rubble piles were approximately 1 m^2 and area of each coral head was calculated as the surface area of a hemisphere. Juvenile bicolor damselfish were collected from the fore reef slope with hand nets and anesthetic (quinaldine). Juveniles were held for 12 hr in a bath of tetracycline

hydrochloride to mark their otoliths (Hettler 1984) and were injected subcutaneously with tattoo ink. After all other *Stegastes* residents were removed, tattooed juvenile *S. partitus* were released onto experimental units at 4 fish/m^2 which is the average natural density of *S. partitus* on coral heads in the surrounding area. The tattoo allowed detection of fish immigrating from experimental units and allowed me to distinguish them from larvae recruiting naturally to the units. Surrounding coral heads were frequently examined for tattooed migrants. Once *S. partitus* densities were established, juvenile beaugregory damselfish (*S. leucostictus*) were added to half the randomly selected experimental units at 5 fish/m^2. This was the natural density of beaugregory damselfish on the back reef.

Table 1. Experimental design in Teague Bay, St. Croix. Design in Jamaica excluded the nested term, therefore the F-ratio for the main effect, Habitat, was calculated as $MS_{(h)}/MS_{(e)}$. $MS_{(e)}$ is the mean square error of the residual. There were four replicates per treatment.

Main Effect	Fixed/ Random	Levels	F-ratio
Habitat (h)	F	back reef vs. fore reef	$MS_{(h)}/MS_{(site\{habitat\})}$
Site {Habitat}	R {nested}	east vs. west	$MS_{(site\{habitat\})}/MS_{(e)}$
Substrata (s)	F	coral vs. rubble	$MS_{(s)}/MS_{(e)}$
Competition (c)	F	0 vs. 5 *S. leucostictus*/m^2	$MS_{(c)}/MS_{(e)}$

The relative supply of planktonic organisms potentially available to juvenile bicolor damselfish during the study period was measured using tube traps (Yund et al. 1991). The clear, cylindrical acrylic tubes (60 cm height x 5.1 cm inside diameter) were filled with a 10% solution of buffered (borax) formaldehyde and sea water with a few drops of food color added. Typically all but the top 10 - 15 cm of the tube remained green indicating that the

majority of the formalin solution was retained. Organisms which drifted in were preserved. Six tube traps were deployed in pairs at each site. One tube of each pair was placed with its opening 1.5 m above the bottom and the second tube with its opening at 0.5 m (Fig. 4). The base of the lower tube was buried 10 cm into the sand. Associated with each pair of tubes was a plaster block intended to obtain a relative measure of flow rate at that site. Dissolution blocks were constructed by pouring plaster of paris into aluminum soda cans which had a screw fastened through a hole in the bottom of the can. Once hardened, the upper part of the can was peeled away leaving a 2 cm aluminum base on which the plaster mold rested. The top was shaved smooth and the sides were coated with varnish. Thus only the top surface area was exposed to water flow creating a uniform dissolution area. As the plaster dissolved the outer varnish flaked off. Blocks were dried in an oven for 24 h then weighed prior to deployment.

The experiment was commenced 23 June, 1993. Every two weeks all species of fish occupying experimental units were censused and juvenile *S. partitus* and *S. leucostictus* were replenished if required to maintain experimental densities. The number of juvenile bicolor damselfish that remained at each census provided an estimate of survival for each two week period. The proportion of juvenile *S. partitus* surviving to the end of the study (total survival rate) was analyzed with a 3-way analysis of variance test (habitat, substrate, competition as main effects) with one nested term (site{habitat}). The F-statistic for the main effect, habitat, was calculated by dividing its mean square error (MS) by the nested term mean square error ($MS_{habitat}/MS_{site\{habitat\}}$, Zar 1984). In the ANOVA tables for growth and survival I have included the variance components that are attributable to the main effects (Sokal and Rohlf 1981).

During the course of the study, the behavior of three juvenile *S. partitus* from each experimental unit was recorded. Data included feeding rate and percent time foraging in planktonic vs. benthic habitats. Every two weeks, tube traps and plaster blocks were retrieved. The formalin solution was filtered through a 75 μm mesh sieve and the planktonic organisms from each tube were stored in individually labeled vials. Plaster blocks were dried in an oven until no further loss in weight occurred. Approximately 36 h was needed for the largest plaster blocks to dry. The difference in initial weight to final weight indicated the amount of plaster dissolved in two weeks. Tube traps with fresh formalin solution and new plaster blocks were replaced the following day. This procedure was repeated 7 July, 22 July, 6 August, and concluded 22 August, 1993.

At the end of the study all remaining fish were collected, measured (±0.05 mm SL), wet weighed (± 0.001 g) and fixed in 10% formalin for 48 hr then transferred to 75% ETOH. Otoliths were dissected out and viewed under ultraviolet light at 400 - 600 magnification. Growth was measured as the increase in otolith radius from tetracycline mark (it fluoresces under UV light) to edge of the otolith using a digitized video image. Otolith growth rates of fish from each experimental unit were averaged to obtain a single datum point per replicate. These data were analyzed with a 3-way, nested ANOVA (habitat, substrate, competition, site{habitat}). The F-statistic for the main effect, habitat, was calculated by dividing its mean square error by the mean square error of the nested term ($MS_{habitat}/MS_{site\{habitat\}}$). A small sample of juvenile *S. leucostictus* was also collected from the back reef to compare their growth rates with that of *S. partitus*. Tube trap contents were sorted and individual plankton were counted and classified to ordinal level. Only those items which were numerous enough for analysis were compared

with a 2-way nested ANOVA (habitat, trap height, site{habitat}). The f-statistic for the main effect, habitat, was calculated as above.

An identical experiment to the one just described, with two exceptions, was conducted in Discovery Bay, Jamaica. Since the back reef of Discovery Bay contained a single suitable location which met the criteria used in St. Croix (e.g. isolated *M. annularis* coral heads surrounded by sand), only one site on the back reef and adjacent fore reef was used. Second, due to logistical difficulties and time constraints, tube traps and plaster blocks were not deployed. The experiment in Discovery Bay commenced on 28 January, 1994. After two weeks , juvenile bicolor and beaugregory damselfish were censused and restocked (11 Feb.) to starting densities. All remaining bicolor damselfish were collected and preserved on 26 February. Since the experiments in St. Croix and Jamaica ran for different lengths of time (8 vs. 4 wk), I used the average two-week mortality estimates to compare survival rates among islands. Survival rates and otolith growth rates were analyzed with a 3-way ANOVA.

RESULTS

Morphological characteristics of the experimental units used in St. Croix varied slightly among habitats and between sites within habitats. Coral heads were slightly smaller on average at WFR and EBR (Table 2A). The back reef lacked other small coral varieties and sponges, whereas on the fore reef, the macroalgae *Dictyota divaricata* often covered portions of rubble piles (Table 2A, B). In Jamaica, coral head area (± s.e.) averaged 1.28 (±0.174 s.e.) m^2 on the

fore reef and 1.96 (0.318 s.e.) m^2 on the back reef with no macroalgae growing on the rubble piles.

Table 2. Substrate characteristics (mean ±s.e.) of A) *Montastrea annularis* coral heads (n=8) and B) *Porites* rubble piles (n=8) at each location within Teague Bay study site: east fore reef (EFR), west fore reef (WFR), east back reef (EBR) and west back reef (WBR). % is percent cover, # is number of individual gorgonians, coral colonies and sponges.

A

Coral Substrate	EFR	WFR	EBR	WBR
Mean Area (m^2)	2.58 (0.22)	1.66 (0.14)	1.92 (0.31)	3.74 (0.67)
% Live *Montastrea*	30.0 (5.34)	46.3 (5.32)	38.1 (3.77)	46.5 (7.26)
% Dead *Montastrea*	36.9 (7.50)	18.4 (5.04)	36.9 (5.26)	22.1 (3.40)
% Macro algae	27.6 (4.91)	33.2 (3.65)	22.2 (4.99)	27.1 (5.66)
% Sessile organisms	5.5 (1.48)	2.1 (1.12)	2.8 (1.75)	3.5 (2.38)
# Gorgonians	3.0 (0.76)	1.6 (0.68)	1.5 (0.53)	0.8 (0.8)
# Coral	5.6 (1.57)	1.6 (0.84)	0.2 (0.16)	0
# Sponges	2.2 (0.82)	4.4 (0.60)	0	0

B

Rubble Substrate	EFR	WFR	EBR	WBR
% Bare Rubble	60 (9.16)	46.2 (7.83)	98.8 (1.25)	91.2 (2.95)
% Macro algae	40 (9.16)	57.8 (7.83)	1.2 (1.25)	8.8 (2.95)

In both Teague Bay and Discovery Bay, juvenile *S. partitus* showed depressed growth rates living on the back reef (Fig. 5) and in the presence of the territorial competitor, *S. leucostictus* (Fig. 6). These two factors accounted for 48.5% and 32.2% of the variation in growth in St. Croix and Jamaica, respectively (Table 3). Moreover, fish grew at slower rates living on *M. annularis* coral heads than on *Porites* rubble although this trend was only significant in Teague Bay (Fig. 7). In St. Croix, differences in growth among sites within each reef habitat were non-significant (P=0.078). However, the nested term was not removed from the model due to the probability of

committing a Type II error. As recommended by Winer (1971), a conservative approach to pooling can be used when the F-ratio is non-significant at P=0.25 instead of the usual P=0.05 (Underwood 1981). Comparison of interspecific growth rates on the back reef of St. Croix indicated that *S. leucostictus* grew nearly twice as fast as *S. partitus* (0.16 vs. 0.09 mm/d SL, $F_{(1, 21)}$, $P < 0.001$).

Table 3. Results of 3-way, nested analysis of variance of fish growth in Teague Bay, St. Croix and Discovery Bay, Jamaica. * $P \leq 0.05$, ** $P \leq 0.01$. Amount of variance accounted for by each component are listed as percentages. See Table 2 for explanation of treatments.

St. Croix

Source	d.f.	M.S.	F	P	% Variance
Habitat (H)	1	7.574	20.880	0.045*	30.2
Site {Habitat}	2	0.363	2.678	0.079	3.7
Substrata (S)	1	0.835	6.168	0.016*	11.9
Competition (C)	1	1.218	8.992	0.004**	18.3
H x S	1	0.025	0.182	0.672	0
H x C	1	0.035	0.262	0.611	0
S x C	1	0.003	0.022	0.882	0
H x S x C	1	0.147	1.082	0.303	0.1
Error	54	0.135			35.8

Jamaica

Source	d.f.	M.S.	F	P	% Variance
Habitat (H)	1	1.444	4.414	0.048*	7.4
Substrata (S)	1	0.902	2.757	0.112	3.9
Competition (C)	1	4.117	12.589	0.002**	24.8
H x S	1	0.695	2.125	0.160	4.8
H x C	1	1.061	3.244	0.086	9.6
S x C	1	0.018	0.055	0.817	0
H x S x C	1	0.756	2.321	0.143	11.2
Error	21	0.327			34.3

Overall feeding rates (bites/min $\pm$ s.e.) of juvenile *S. partitus* in St. Croix were similar among reef habitats (fore = 10.1 $\pm$ 3.75, back = 11.0 $\pm$ 4.86). However, fish living on the fore reef had a significantly greater proportion of their feeding concentrated in the plankton than fish on the back reef (80.1%

vs. 68.7%, respectively, $F_{(1,56)} = 7.958$, $P = 0.007$). Foraging patterns may have reflected the relative supply of planktonic food to the fore reef and back reef habitats. Of the diversity of organisms captured in the tube traps, only the most abundant were included for analysis (Table 4). Although variation in supply of different organisms occurred during the three sample periods (Fig. 8) these were pooled for analysis since fish growth rates were averaged over the entire summer study period. Total plankton supply was 46% greater on the fore reef relative to back reef locations, with copepods numerically dominating the tube trap samples (Fig. 9). Several of the organisms that are eaten by bicolor damselfish were more abundant on the fore reef (Fig. 10). All organisms showed similar densities among sites within reef zones except cumaceans, which were significantly more abundant at east fore reef, and bivalves, which were significantly more abundant at west fore reef (Table 4). Among trap heights, ostracods, foraminiferans and algal fragments were more abundant in the 0.5 m traps, whereas calanoid copepods and *Oikopleura* were more abundant in the 1.5 m traps (Table 4). Although a few types are truly pelagic (e.g. calanoid copepods, *Oikopleura* larvaceans) many probably entered the traps during their diel vertical migrations or were suspended into the water column during heavy wave activity. Other organisms captured in the traps but not analyzed included euphausids, chaetognaths, cnidaria, larval cephalopods, larval fish, larval ascidians, larval echinoderms, nematodes, sipunculids, barnacle cyprids and one very dumb adult redband parrotfish (*Sparisoma aurofrenatum*). There was no difference in dissolution of plaster blocks between fore and back reef of St. Croix. The large amount of oscillatory flow near the back reef crest could have contributed to this result.

Table 4. Results of separate 2-way analyses of variance of plankton abundance during study. Main effects are Reef Habitat (fore, back), Trap Height (0.5 m, 1.5 m) and Location (east, west) nested within Habitat. * $P \leq 0.05$, ** $P \leq 0.01$.

Organism	Habitat	Location {Habitat}	Trap Height	Habitat x Height
	$F_{(1, 66)}$, P	$F_{(2, 66)}$, P	$F_{(1, 66)}$, P	$F_{(1, 66)}$, P
Calanoid copepod	17.06, 0.05*	1.25, 0.29	4.72, 0.03*	0.01, 0.93
Cyclopoid " "	43.76, 0.02*	2.10, 0.13	0.83, 0.37	0.07, 0.79
Harpacticoid "	0.86, 0.45	1.27, 0.29	1.25, 0.27	4.19, 0.04*
Oikopleura	254.0, 0.01**	0.20, 0.82	43.4, 0.01**	14.6, 0.01**
Gastropods	0.06, 0.83	2.90, 0.06	0.01, 0.92	0.18, 0.68
Polycheates	1.44, 0.35	0.61, 0.55	1.03, 0.31	0.45, 0.50
Mysids	9.29, 0.09	1.88, 0.16	0.37, 0.54	0.97, 0.33
Decapods	0.85, 0.45	0.58, 0.56	0.34, 0.56	1.77, 0.19
Ostracods	278.0, 0.01**	0.11, 0.89	4.95, 0.03*	8.16, 0.01**
Cumaceans	22.1, 0.04*	3.67, 0.03*	3.90, 0.05*	0.87, 0.35
Foraminiferans	15.4, 0.06	2.63, 0.08	9.85, 0.01**	9.31, 0.01**
Isopods	0.20, 0.70	1.19, 0.31	0.23, 0.63	0.47, 0.50
Eggs	0.79, 0.47	1.11, 0.34	0.35, 0.55	0.18, 0.67
Bivalves	3.53, 0.20	6.12, 0.01**	1.50, 0.23	1.5, 0.23
Algal fragments	18.4, 0.05*	0.33, 0.72	0.67, 0.42	0.81, 0.37
Amphipods	0.12, 0.76	2.37, 0.10	0.08, 0.78	4.83, 0.03*

Patterns of survivorship mirrored patterns of growth in both St. Croix and Jamaica. Substrate type had the greatest effect on mortality and accounted for 30.9 and 56% of the variance in St. Croix and Jamaica (Table 5). Fish living on *Porites* rubble survived better than fish living on *Montastrea* coral in both Teague Bay and Discovery Bay (Fig. 11). Interspecific competition and the back reef habitat reduced juvenile survival in St. Croix and accounted for 18.7 and 8.8% of the variation. No significant difference in survivorship was detected among these main effects in Jamaica (Figs. 12, 13).

During the periodic censuses of the experimental units, counts of all potential fish predators were made. It must be emphasized that the predator counts were done during daytime hours within my study area which consisted of isolated coral heads and rubble piles surrounded by sand. Some

predators prefer this type of environment (groupers, lizardfish) whereas others (trumpetfish) occur more commonly on the contiguous reef. Criteria for identifying potential predators were based upon Randall's (1967) gut content analysis of Caribbean reef fishes. All species which had greater than 20% gut volume represented by fish were considered potential predators in addition to species I observed eating bicolor damselfish. These potential predators included groupers (Serranidae: *Epinephelus guttatus, E. adscensionis, Cephalopholis cruentata, C. fulvis*), lizardfish (Synodontidae: *Synodus intermedius*), trumpetfish (Aulostomidae: *Aulostomus maculatus*), moray eels (Muraenidae: *Gymnothorax moringa, G. miliaris, G. funebris*), hamlets and other small serranids (Serranidae: *Hypoplectrus* spp., *Serranus tigrinus, S. tabacarius*), and snappers (Lutjanidae: *Lutjanus apodus, L. mahogoni, Ocyurus chrysurus*). The density of these predators was similar among reef habitats in St. Croix but was very different among reef habitats in Jamaica (Fig. 14). In Jamaica *E. guttatus* was the primary piscivore on the fore reef. It was an effective predator especially when it foraged in groups of two or three individuals. Several predation events on juvenile bicolor damselfish were observed to occur in this manner.

The additive effects of reef habitat, substrate type and interspecific competition on growth and survival were evident in both St. Croix and Jamaica (Fig. 15). With few exceptions, growth and survival declined for fish transplanted to the back reef, to coral substrate or to the presence of a territorial competitor. In Jamaica the larger variation in growth and survival among experimental treatments partly reflects the abbreviated study duration (4 vs. 8 wk) but also the reduced number of surviving damselfish due to higher site-specific predation intensity (Fig. 14).

Table 5. Results of 3-way, nested analysis of variance of fish survival in Teague Bay, St. Croix and Discovery Bay, Jamaica. Amount of variance accounted for by each component are listed as percentages. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

St. Croix

Source	d.f.	M.S.	F	P	% Variance
Habitat (H)	1	71.341	35.657	0.027*	8.8
Site {Habitat}	2	2.001	0.472	0.626	0
Substrata (S)	1	64.748	15.278	0.001***	30.9
Competition (C)	1	39.896	9.414	0.003**	18.7
H x S	1	10.878	2.567	0.115	1.7
H x C	1	3.057	0.721	0.400	0
S x C	1	7.904	1.865	0.178	3.7
H x S x C	1	5.039	1.189	0.280	1.6
Error	54	4.238			34.6

Jamaica

Source	d.f.	M.S.	F	P	% Variance
Habitat (H)	1	3.228	0.571	0.458	0
Substrata (S)	1	130.369	23.073	0.001***	56.0
Competition (C)	1	13.107	2.320	0.143	3.4
H x S	1	0.302	0.053	0.820	0
H x C	1	0.513	0.091	0.766	0
S x C	1	1.915	0.339	0.567	0
H x S x C	1	0.013	0.002	0.962	0
Error	21	5.650			40.6

DISCUSSION

Results of this study indicated that differential survival after settlement was responsible for the differences in the proportion of juveniles and adults among back and fore reef habitats. Slower growth rates may have indirectly influenced mortality in both St. Croix and Jamaica due to limited food resources and elevated competitive interactions. Population size was further reduced under conditions of heavy predation pressure which was habitat and island specific. Although Clarke (1977) and Itzkowitz (1977) were correct in assessing that habitat partitioning among damselfish communities was the result of multiple factors, this study is the first to identify and determine the relative importance of these factors. These complex interactions are discussed in more detail below.

Effects of Reef Habitat on Growth and Survival

When *S. partitus* juveniles were placed on the back reef habitats of Teague Bay, St. Croix and Discovery Bay, Jamaica, growth rates were reduced relative to the fore reef by 32% and 16%, respectively. The process that typically regulates organismal growth is the quantity and quality of food. *Stegastes partitus* feeds on benthic and pelagic material (algae and microinvertebrates) when young but switches to a predominately planktonic diet with increasing age (Stevenson 1972; Emery 1973). Therefore, the supply of planktonic food will become relatively more important to older juveniles. Copepods, which are the only animal food consistently eaten by *S. partitus*

(Emery 1973), were 64% less abundant on the back reef of St. Croix. Reductions in the supply of zooplankton to back reef habitats have been well documented (Glynn 1973; Bray 1981; Gaines and Roughgarden 1987; Hamner et al. 1988; Kingsford and MacDiarmid 1988) and may determine species distribution patterns. For example, plankton-feeding damselfishes (*Chromis* spp.) are restricted to the outer reef slopes whereas algal-grazing damselfishes (*Stegastes* spp.) are largely restricted to shallow reef areas (Allen 1975, Thresher 1983, Nemeth, pers. obs.). *Stegastes partitus* is intermediate between these two trophic types because of its dietary switch. Therefore, settling larvae may not be selecting for their optimum adult habitat but basing their selection of habitats on their immediate dietary needs, benthic algae and invertebrates. Although benthic food supply was not measured, it was assumed to be relatively similar within each substrate type among reef habitats since the same species of live coral and coral rubble were used. Over the course of the study, however, a dense growth of macro algae (primarily *Dictyota divaricata*) covered some of the fore reef rubble piles in St. Croix (Table 2). It is possible that dense algal cover caused an increase in the abundance of invertebrate prey (Gotceitas and Colgan 1989) contributing to greater growth rates. But at the same time, the dominant and unpalatable macro algae would have decreased the biomass of filamentous algae (Hixon and Brostoff 1983) which is preferred by pomacentrids (Emery 1973).

Patterns of survival of juveniles among habitats were influenced by different processes on each island. In St. Croix, increased survival tracked patterns of increased growth (Figs. 5, 12). It is generally agreed that smaller individuals are vulnerable to a larger number of potential predators (Jeffries and Terceiro 1985; Juanes 1994) and that the length of this vulnerable period is inversely proportional to the rate of growth. The limited census of

potential predators suggested that predation pressure was similar among habitats in St. Croix (Fig. 14). Thus, with predation intensity being equal, the overall risk from predators within each habitat would decrease proportionally with increasing size. In gross proportions, the 32% increase in growth on the fore reef was associated with a 20% increase in survivorship. In Jamaica, however, variation in intensity of predation among habitats was the primary factor associated with survivorship patterns (Fig 12). The 20% survival advantage achieved in St. Croix, due to increased growth, was lost in Jamaica due to increased predation pressure. The high density of piscivorous groupers (Fig. 14), in particular the graysby (*Cephalopholis cruentata*), was responsible for increased juvenile mortality (pers. obs.). As a group of two or three groupers approached a coral head, they would split apart, one going up over the head while the others went around the left and right sides. The prey was usually eaten by one grouper as it fled from the attack of a second grouper (pers. obs). The group foraging behavior by *C. cephalopholis* spp. has been reported in Jamaica (Kaufman 1983) and the Red Sea (Shpigel and Fishelson 1989) but was not observed in St. Croix. Opportunistic foraging behavior has been documented in heterospecific groups as well (Aronson and Sanderson 1987).

Effects of Substrate Types on Growth and Survival

In St. Croix and Jamaica fish tended to have faster growth rates (12% and 21%) on rubble substrate. This trend was similar in both habitats. Although fish living on coral heads may have greater access to plankton because of their elevation into the water column (Hobson 1991), there was little difference in plankton abundance among the two heights of tube traps (except calanoid

copepods and *Oikopleura*). It is possible that juvenile bicolor damselfish living on rubble may have greater access to benthic algae and other organisms to supplement their diet when plankton supply may be temporarily limited.

The effect of substrate type on survival rate was quite pronounced. Percent survival decreased by 21% in St. Croix and 44% in Jamaica between *Porites* rubble and *Montastrea* coral substrates. The number and size of available refuges likely contributed to this result (Chap. 2). Crevice size averaged 15.9 cm^2 (±4.26 s.d., range = 7.6 - 24.8) for rubble and 48.5 cm^2 (±21.27 s.d., range = 20.7 - 101.6) for *Montastrea*. Moreover, crevice density averaged 39.5/m^2 (±5.40 s.d., range = 25 - 53) for rubble and 14.3/m^2 (±6.27 s.d., range = 4.4 - 34.3) for *Montastrea*. The ability of prey species to avoid being eaten is strongly correlated to the number of available prey refuges and the density of predators (Hixon 1991) with a negative relationship between the number of predators and the maximum number of co-occurring prey (Hixon and Beets 1989, 1993).

Effects of Interspecific Competition on Growth and Survival

The presence of *S. leucostictus* reduced *S. partitus* growth by 14% in St. Croix and 26% in Jamaica. Slowed growth may have resulted from increased competition for food and shelter. Higher densities of territorial fishes may increase territorial aggression with neighbors or may limit access to food resources. Emery (1973) reported that juveniles (<30 mm SL) of *S. leucostictus* (n=7) fed primarily on harpacticoid copepods (50%), nemerteans (24%), polychaetes (18%), and benthic algae (7%) while *S. partitus* (n=7) fed primarily on benthic algae (72%), copepods (15%), pelagic algae (6%), and insect larvae (5%). Although these data indicate that dietary overlap is

limited, stomach contents of these individuals may have reflected the particular reef habitat in which they were collected. Although this information was not provided by Emery (1973), it is likely that *S. leucostictus* and *S. partitus* specimens were collected from their primary habitats, the back reef and fore reef slope, respectively. Therefore aggression among these territorial damselfishes was possibly related to both defense of their shelter and protection of their food supply. Persistence of *S. partitus* living with *S. leucostictus* was reduced by 11% in St. Croix and 18% in Jamaica. As aggressive interactions escalate, growth is reduced since less time is spent feeding and more energy used for defense. Mortality can be increased from the combined effects of slowed growth and reduced vigilance for predators (Shulman 1985a, b; Booth 1995, Jakobsson et al. 1995). Aggression in territorial damselfishes is size dependent where larger individuals within and among species are competitively superior to smaller individuals (Itzkowitz 1977; Robertson 1995). In back reef habitats, *S. leucostictus* grows nearly twice as fast as *S. partitus*. If individuals of both species settled at the same time and same size, *S. leucostictus* would soon become competitively dominant over *S. partitus* due to its accelerated size advantage. Robertson (1995) found that among two co-occurring Caribbean pomacentrids, *S. diencaeus* grows faster and to a larger size than *S. dorsopunicans* and can aggressively take over the living space of the smaller species. During aggressive encounters between *S. partitus* and *S. leucostictus*, I observed that larger damselfish would chase smaller ones up to 10 cm off of the substrate. The smaller fish would return to shelter only after the larger fish resumed feeding. These aggression-derived episodes may make small juveniles extremely vulnerable to predation especially on isolated patch reefs where the surrounding substrate provides minimal shelter.

Cumulative Effects of Biological and Physical Conditions

Benthic processes begin acting at settlement and affect different species in many different ways. When larvae settle onto a coral reef, spatial variation of a range of factors such as shelter and food supply together with the number of predators and competitors, can affect different demographic parameters and these effects change with ontogeny (Jones 1991). The success of settling larvae can produce conspicuous spatial patterns of abundance and distribution of recruits (Sale 1976, Sale et al. 1980, Shulman et al. 1983, Sweatman 1985, 1988; Forrester 1990, Sweatman and St. John 1990) and can ultimately affect local population structure (Connell 1985, Labelle and Nursall 1985, Raimondi 1990, 1991; Choat and Bellwood 1991, Connell and Jones 1991). Moreover, different species will respond directly or indirectly to various physical and biological attributes of the environment producing detectable patterns of distribution among habitats (Jennings et al. 1996). The additive effects of the factors used in this study were readily apparent and can account for the patterns of distribution and population structure of *S. partitus*. With few exceptions, growth and survival of juvenile *S. partitus* declined for fish that were transplanted to the back reef, to coral substrate or included the presence of a territorial competitor. These three factors accounted for 60% and 36% of the variance in growth and 58% and 59% of the variance in survival in St. Croix and Jamaica, respectively.

When *S. partitus* larvae recruit naturally to back reef habitats they are exposed to high levels of interspecific competition especially from the abundant beaugregory damselfish. *S. partitus* displays uni-modal settlement whereas *S. leucostictus* displays bi-modal settlement arriving twice per lunar

cycle typically around the new and full moon (Robertson et al. 1988, 1990). The potential effect of bi-modal settlement is a greater number of *S. leucostictus* individuals arriving over time. Experimental units on the back reef were often colonized by beaugregory damselfish through migration and recruitment. Over a two month period I removed 671 beaugregory recruits from 20 0.5 m^2 rubble piles placed on the back reef. This large rate of influx of *S. leucostictus*, together with its faster rate of growth, will severely limit fitness potential of juvenile *S. partitus*. If *S. partitus* is released from the effects of competition it has the potential to increase its numbers over time (Robertson 1996). Release from competition has been shown to increase temperate reef fish populations as well (Schmitt and Holbrook 1990). As juveniles age, the back reef habitat, which provided sufficient benthic food for newly settled larvae, becomes less habitable as their need for a planktonic diet increases. The combination of these effects will severely limit *S. partitus* populations in back reef habitats and can account for the patterns of population structure found among fore and back reef habitats throughout this species' geographic range (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Whether such biological and physical factors interact to influence the distribution and population structure of other reef fishes will need to be tested. It is likely, though, that the relative magnitude of such effects are more pronounced on strongly site-attached species such as pomacentrids. More mobile species, some of which use schooling as a predator defense mechanism (Pitcher 1986), will most likely migrate greater distances to those habitats that best fulfill their needs during ontogeny.

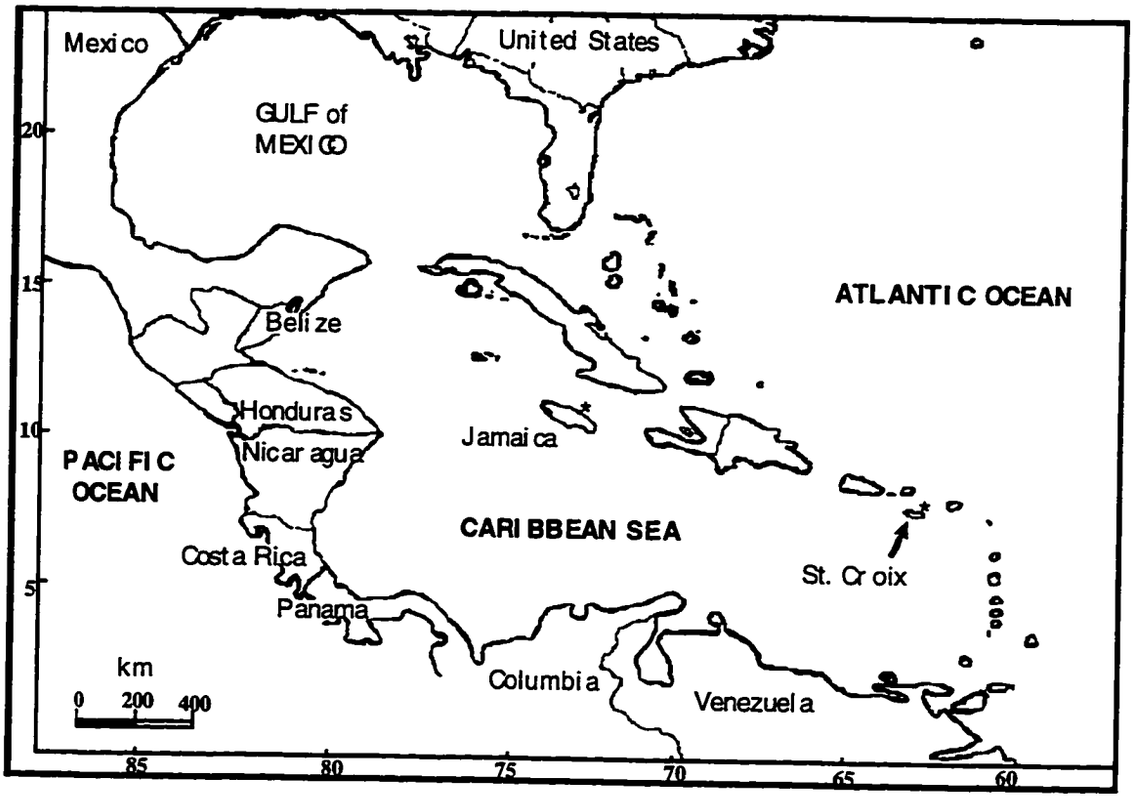

Figure 1. Map of Caribbean. Asterisks indicate approximate location of study sites in Teague Bay, St. Croix and Discovery Bay, Jamaica.

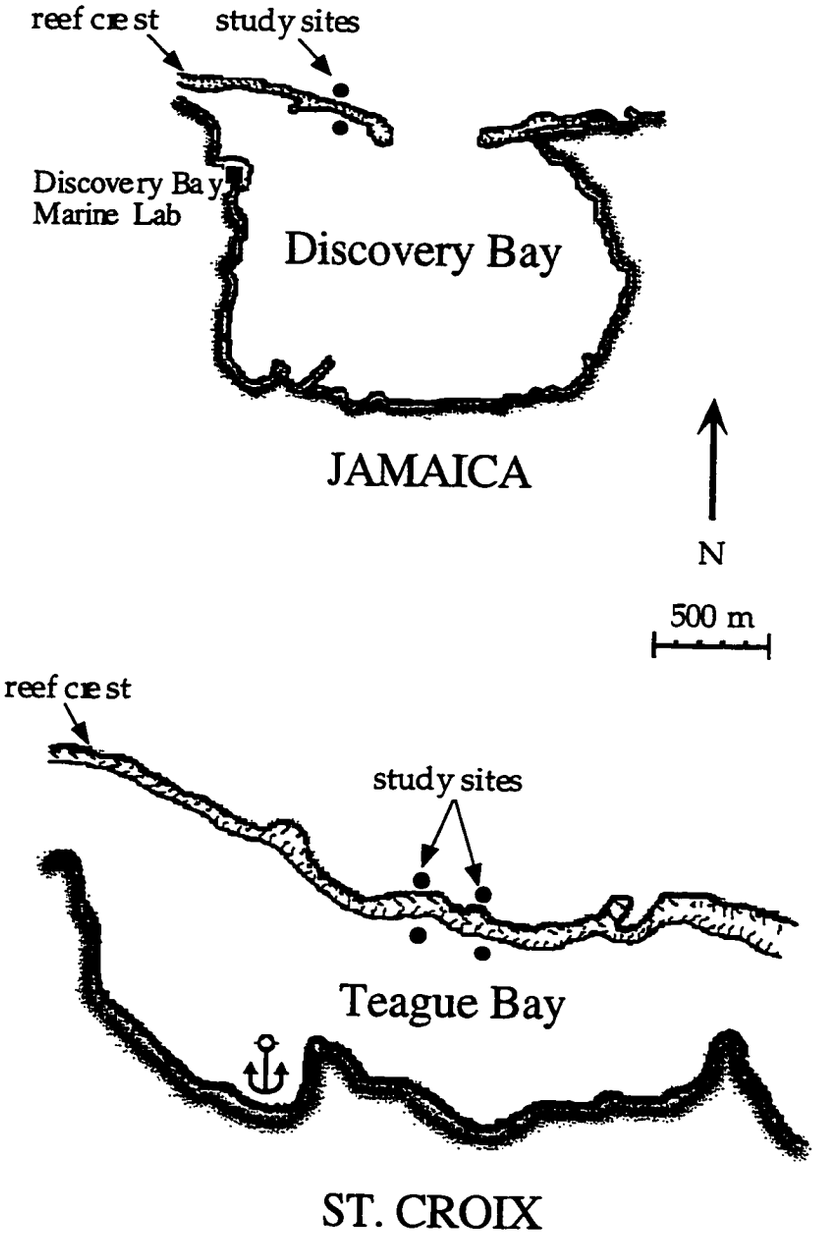

Figure 2. Location of study sites on the fore reef and back reef zones of Teague Bay, St. Croix and Discovery Bay, Jamaica. Anchor indicates location of St. Croix Yacht Club.

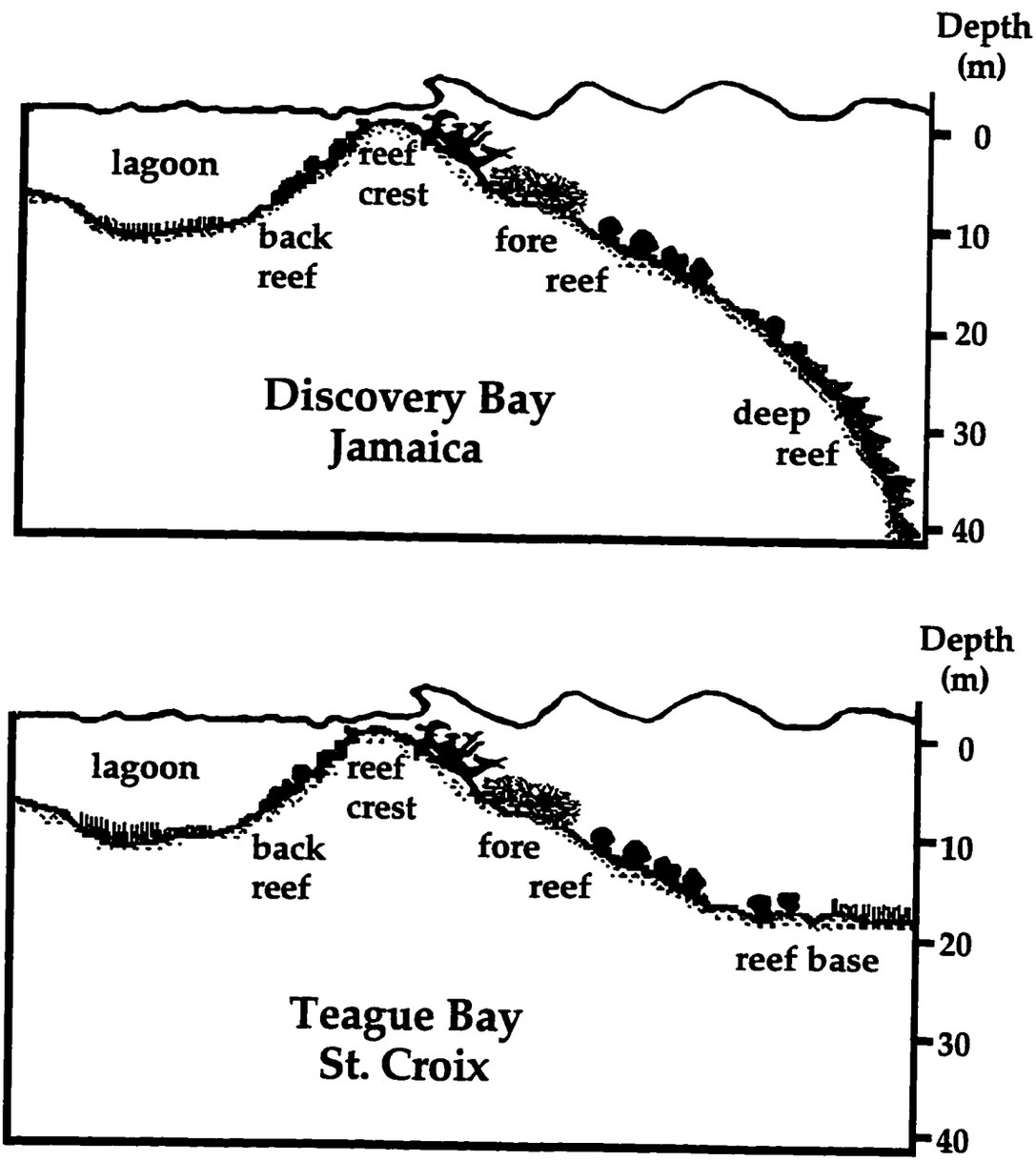

Figure 3. Reef profiles of Discovery Bay, Jamaica and Teague Bay, St. Croix showing typical zonation of major reef building corals. Corals on fore reef from crest are *Acropora palmata*, *A. cervicornis* and *Porites porites*, *Montastrea* spp., and plating *Montastrea* and *Agaricia* spp. on deep reef. Back reef corals include *Montastrea* spp., *Siderastrea* spp., and *P. porites*. Corals enlarged to show detail.

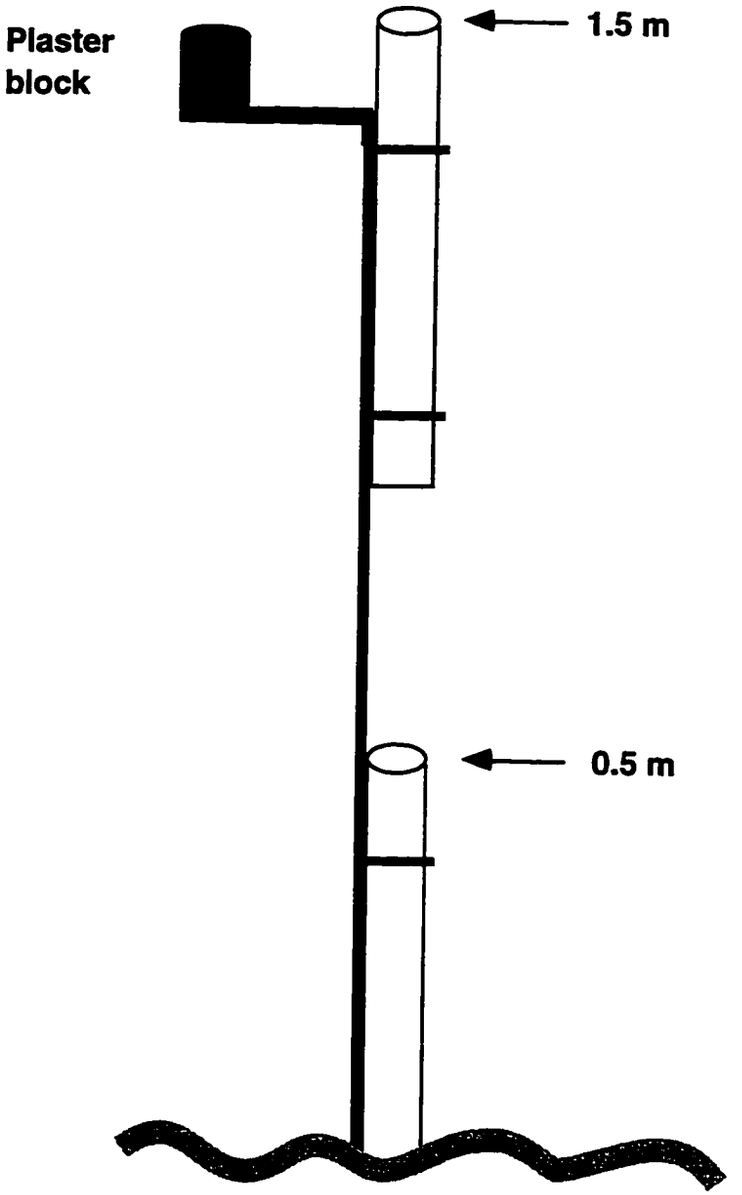

Figure 4. Schematic diagram of plankton collecting tube traps (60 cm x 5.1 cm inside diameter) and associated plaster dissolution block. Tube traps were filled with 10% buffered formalin solution and attached to steel reinforcement bars driven into sand.

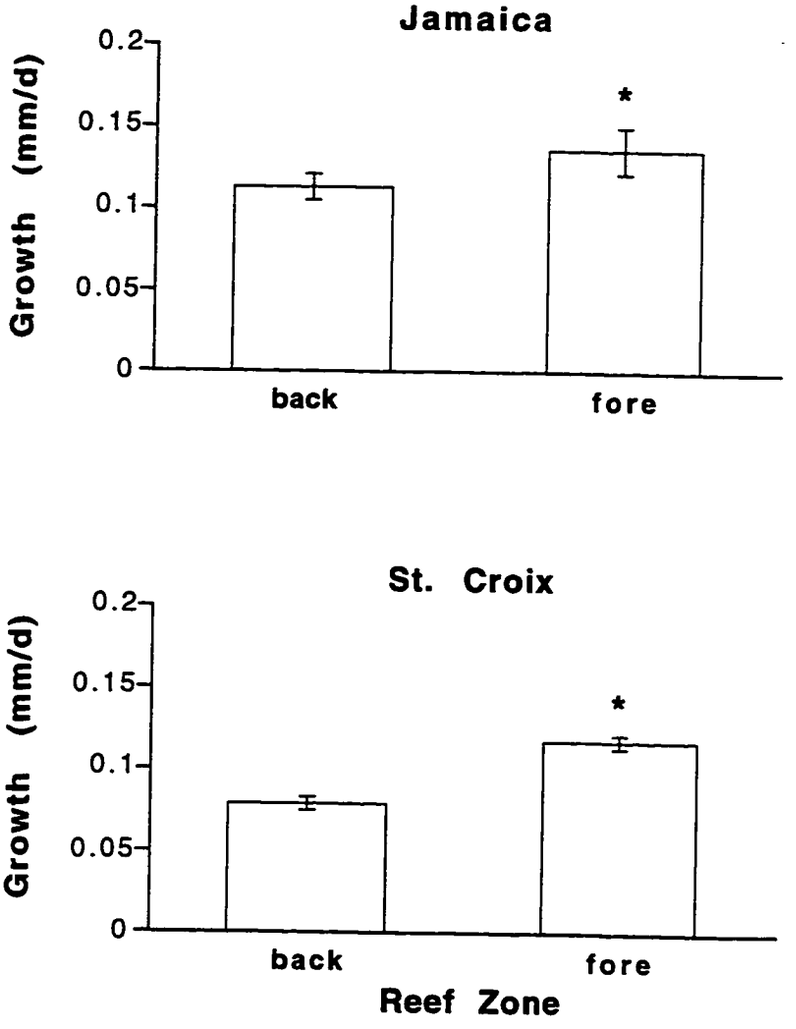

Figure 5. Average growth rate (± 1 standard error = s.e.) in standard length (SL) of juvenile *S. partitus* among back and fore reef zones in St. Croix and Jamaica. * $P < 0.05$.

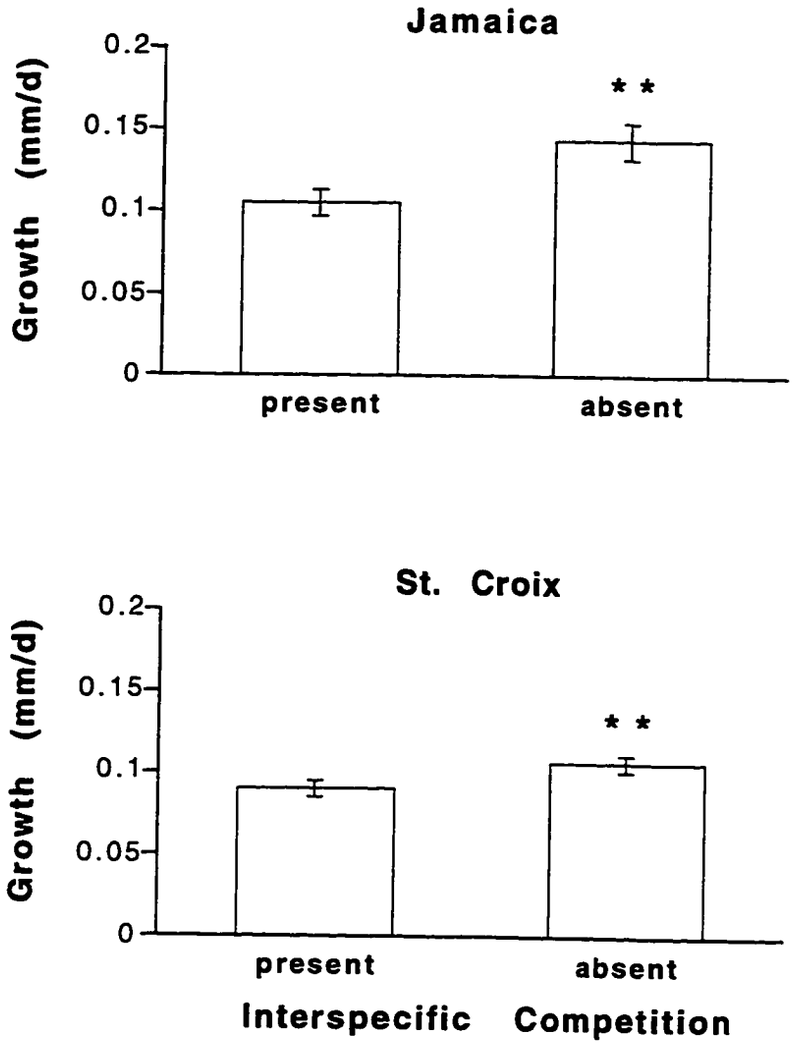

Figure 6. Average growth rate (SL ± 1 s.e.) of juvenile *S. partitus* with or without *S. leucostictus* present. Level of interspecific competition was either 0 or 5 fish/m^2 in St. Croix and Jamaica. ** $P < 0.01$.

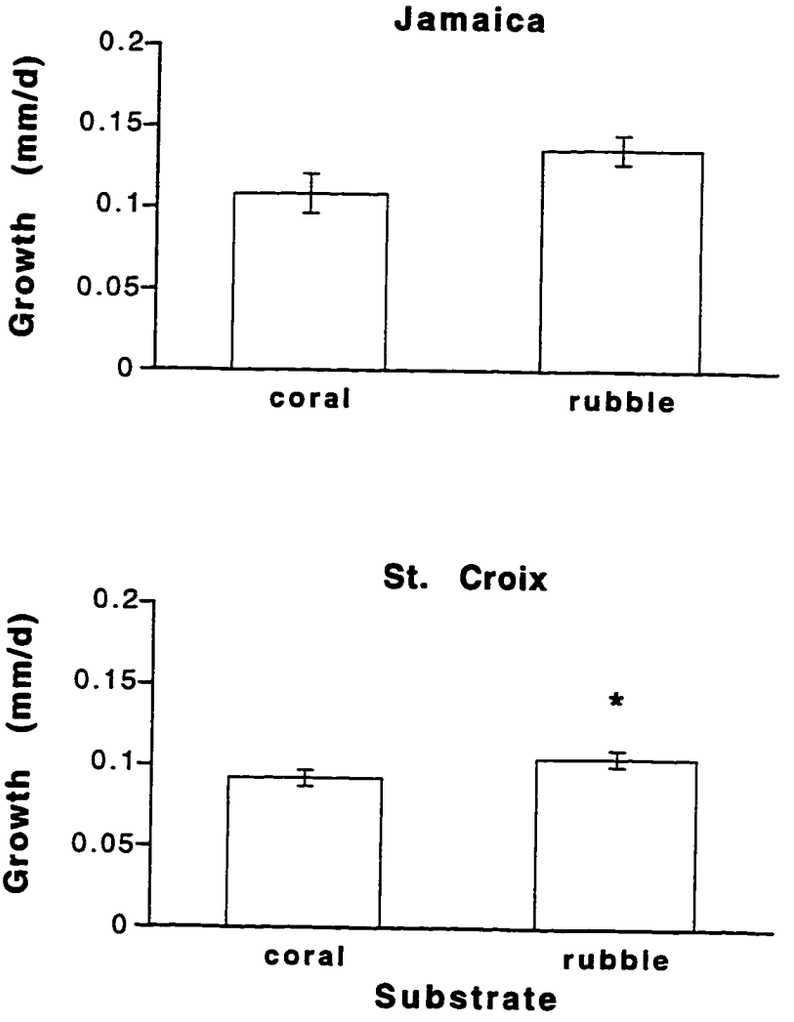

Figure 7. Average growth rate (SL ± 1 s.e.) of juvenile *S. partitus* on *Montastrea* coral or *Porites* rubble in St. Croix and Jamaica. * $P < 0.05$.

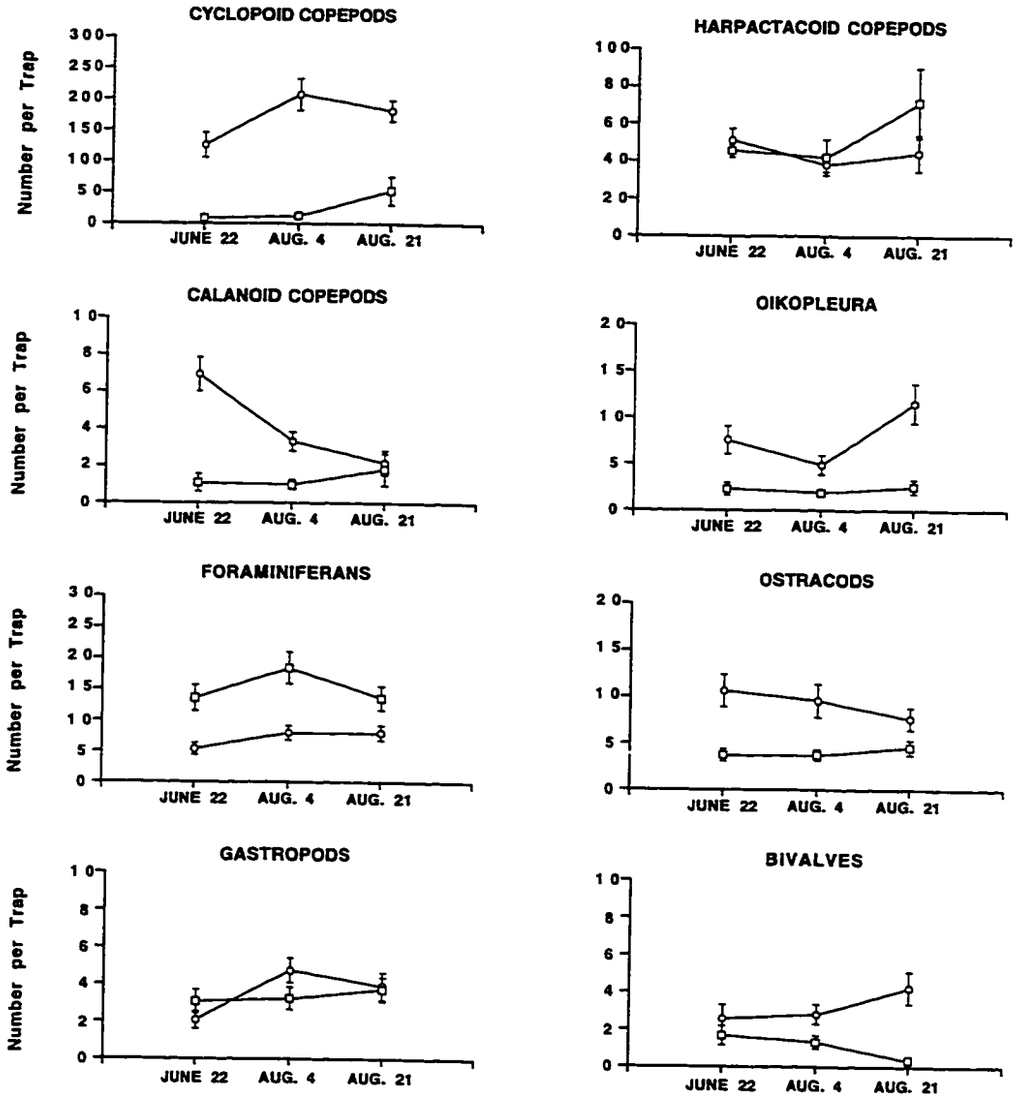

Figure 8. Mean values (± 1 s.e.) of the most common plankton captured in tube traps (n=12) from fore reef (circles) and back reef (squares) zones in Teague Bay, St. Croix. Note difference in y axis scales.

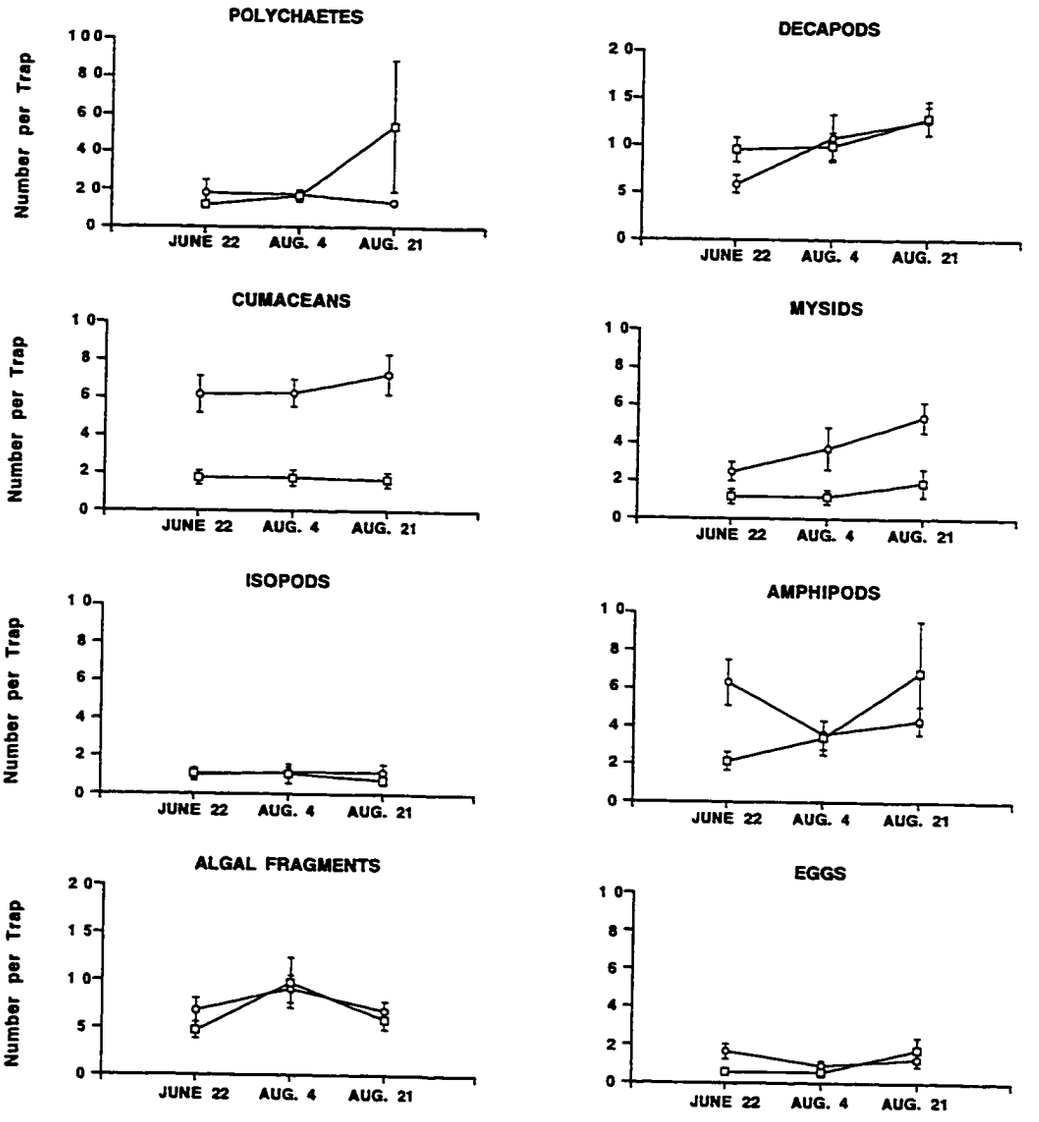

Figure 8. continued

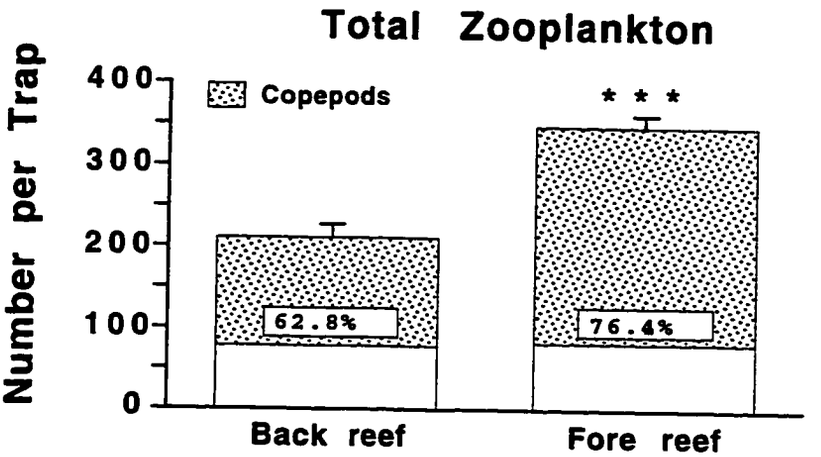

Figure 9. Average number of zooplankton per tube trap (± s.e.) from back and fore reef zones. Shading indicates percent of total plankton catch that was represented by copepods.

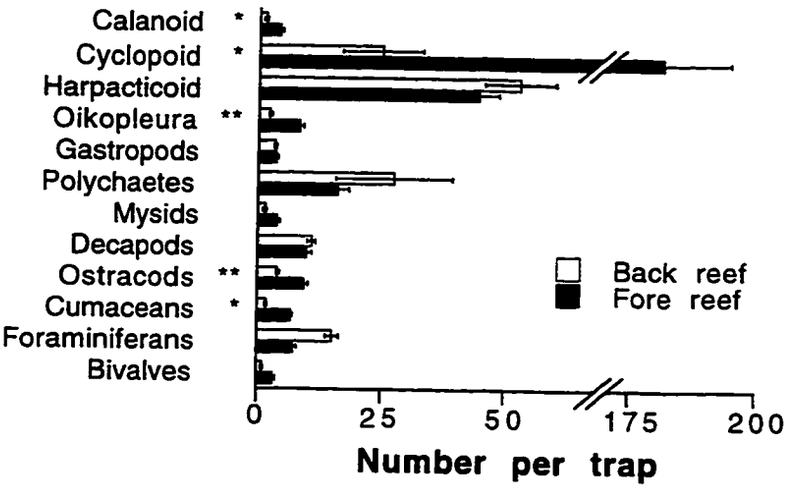

Figure 10. Mean number of planktonic organisms per tube trap (± s.e.) from back reef and fore reef zones averaged for the three sample dates (n=36). Organisms are listed in order (top to bottom) of decreasing dietary importance based on stomach content analyses by Emery (1973) and author. * $P < 0.05$, ** $P < 0.01$.

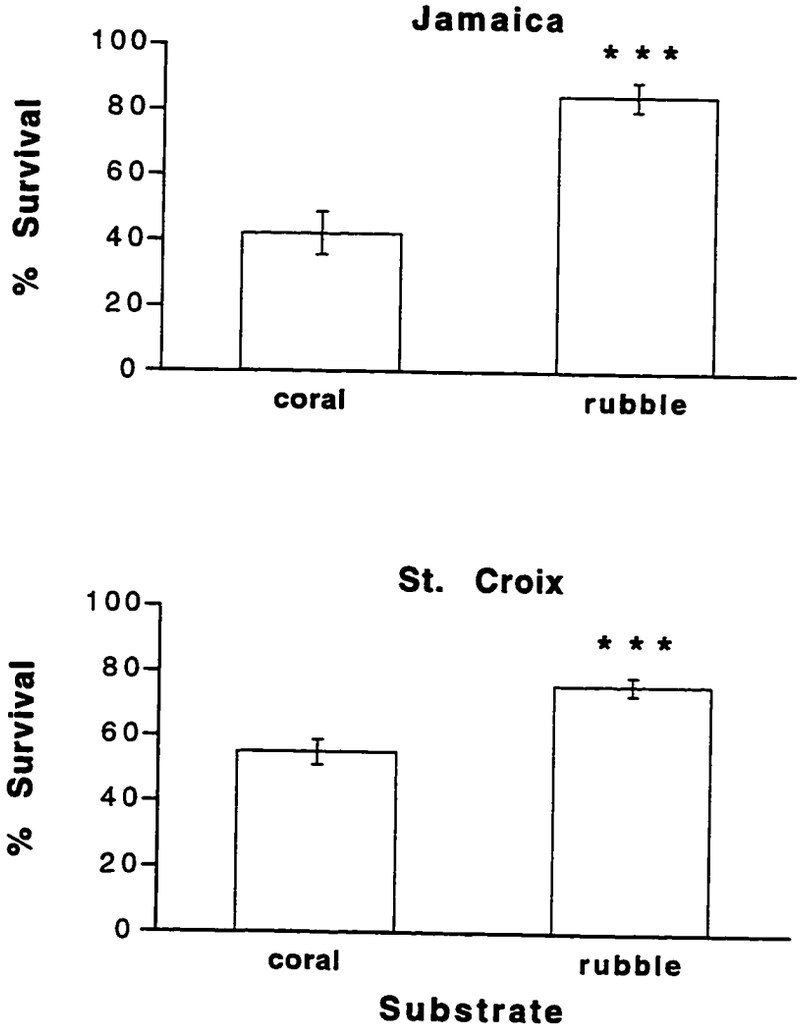

Figure 11. Percent survival rate (± 1 s.e.) of juvenile *S. partitus* on *Montastrea* coral and *Porites* rubble in St. Croix and Jamaica. Survival data were averaged over two week intervals to allow comparison between different study durations in St. Croix (2 months) and Jamaica (1 month). *** P< 0.001.

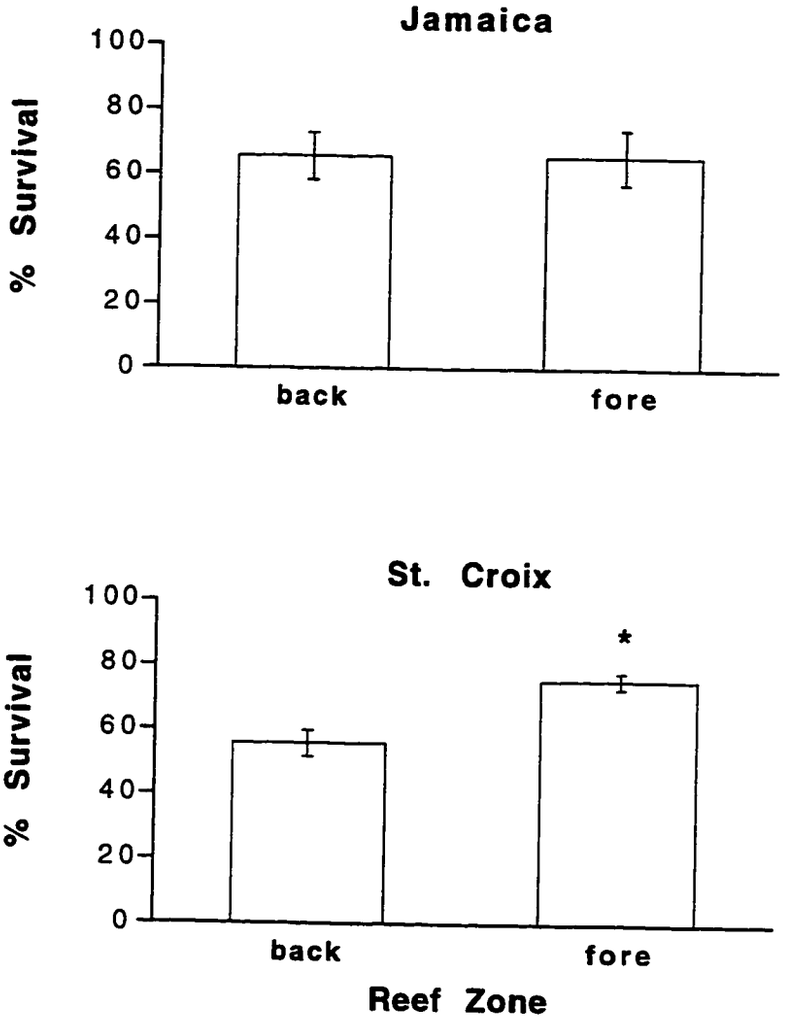

Figure 12. Percent survival rate (± 1 s.e.) of juvenile *S. partitus* among back reef and fore reef zones in St. Croix and Jamaica.
* $P < 0.05$. Data averaged as in Figure 11.

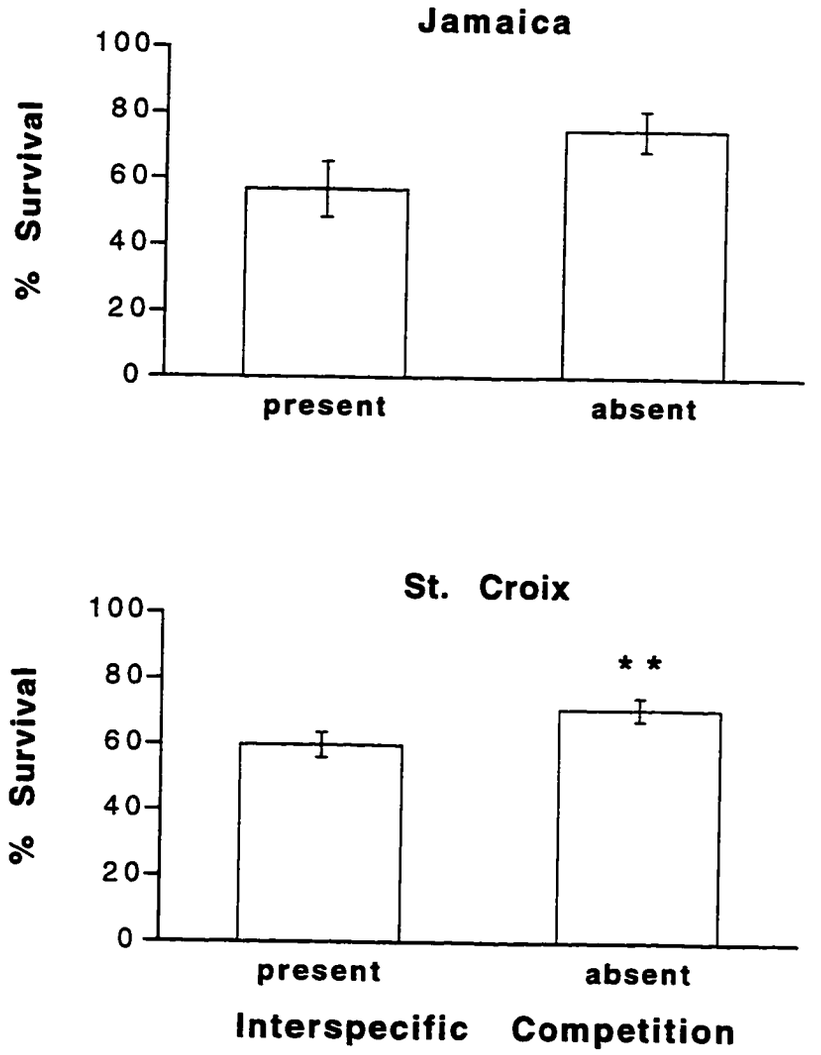

Figure 13. Percent survival rate (± 1 s.e.) of juvenile *S. partitus* with or without *S. leucostictus* present. Level of interspecific competition was either 0 or 5 fish/m^2 in St. Croix and Jamaica. ** $P < 0.01$. Data averaged as in Figure 11.

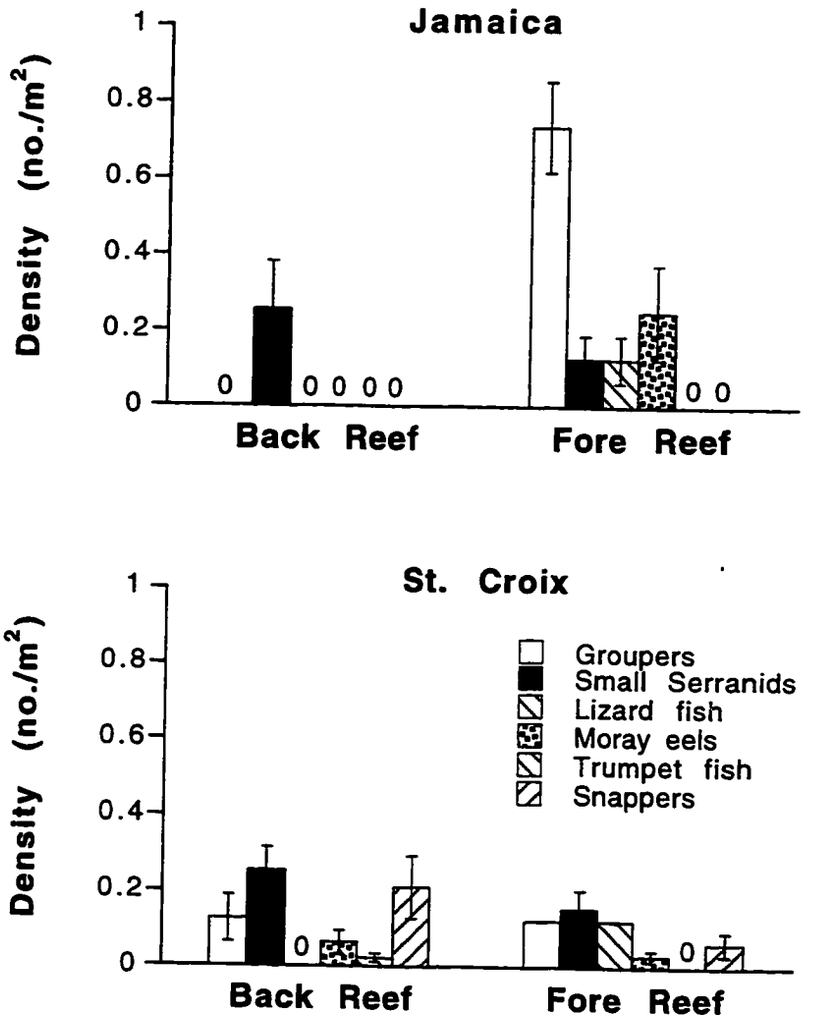

Figure 14. Mean (± 1 s.e.) density of potential predators counted within back reef and fore reef habitats in St. Croix and Jamaica.

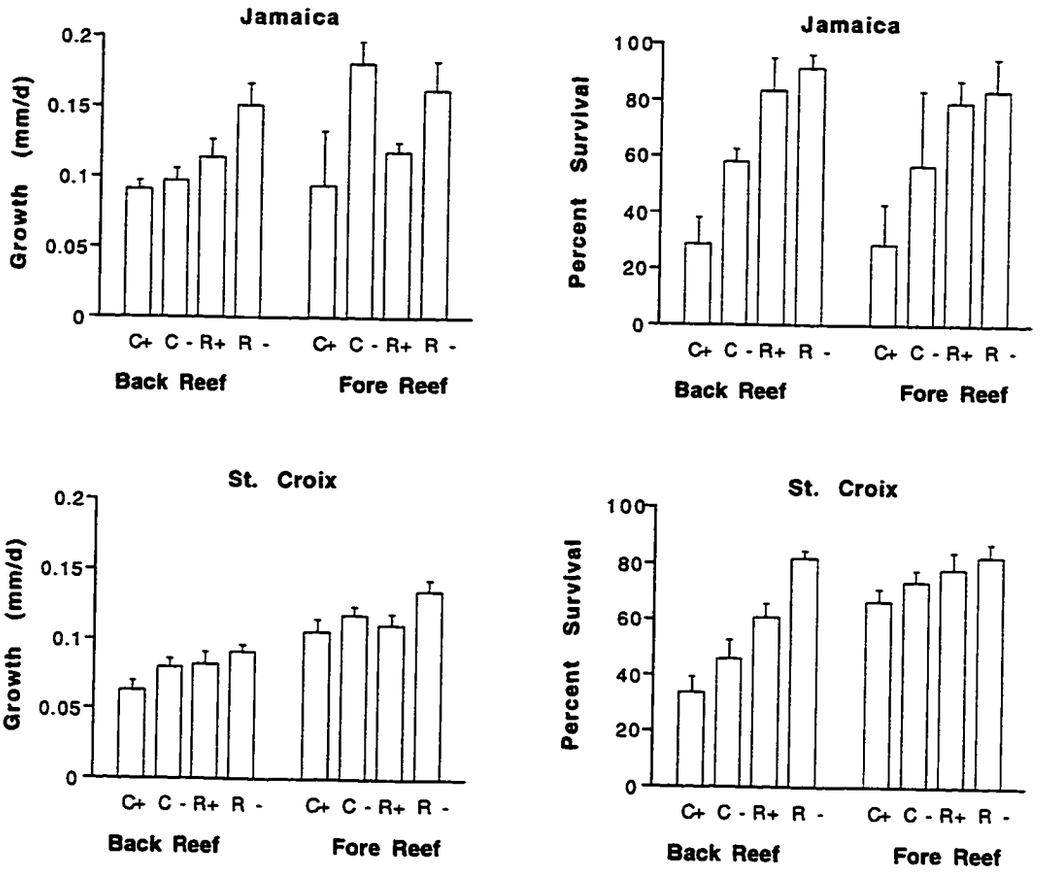

Figure 15. Summary of demographic data showing the additive effects of different experimental conditions on growth rates (SL) and percent survival of juvenile *S. partitus* in St. Croix and Jamaica. Data are mean growth and mean percent survival with standard error bars. C=coral, R=rubble, + = presence of *S. leucostictus*, - = absence of *S. leucostictus*. Ideal conditions for juvenile fish steadily decreased from fish living on the fore reef in *Porites* rubble without interspecific competitors (R-) to fish living on the back reef on *Montastrea* coral with interspecific competitors (C+).

CHAPTER IV

SURVIVAL AND POTENTIAL FITNESS ADVANTAGES TO ONTOGENETIC HABITAT SHIFTS IN THE BICOLOR DAMSELFISH

SUMMARY

Changes in habitat use are associated with patterns of resource use and risk of predation during ontogeny. In this chapter, I show that bicolor damselfish (*Stegastes partitus*) size classes are uniquely distributed among available substrates and that this distribution pattern influences survivorship. In St. Croix, microhabitat analysis of damselfish territories showed that juveniles were positively associated with small coral rubble (< 2 cm diameter). Adults were more widely distributed among different substrates but occurred most frequently on large rubble and on live *Porites* and *Montastrea* corals. Subadult distributions were intermediate between adults and juveniles. To test the effect of small rubble substrate on juvenile recruitment and population size, I added 0, 10 or 20 piles of rubble to 12 large quadrats (15m x 15m) on the fore reef base of Teague Bay and monitored subsequent recruitment. After a 5 month period larval *S. partitus* which initially settled onto small rubble and then shifted to coral had 4 times greater survivorship than larvae which settled directly to *M. annularis* coral (32% vs. 8 %). Juveniles recruiting to rubble shifted to the adult substrate (*M.*

annularis) at a size of 20 to 26 mm SL and as early as two weeks after settlement. These fish moved an average distance of 1.5 m and their direction was often toward conspecific adults. At the population level, there was a positive trend between rubble density and total juvenile recruitment after 2.5 month and 7.5 month period. I interpret the patterns of substrate use by *S. partitus* with a model that predicts the size at which the shift should occur.

INTRODUCTION

In fishes, growth during ontogeny causes individuals to pass through several size-related ecological relationships within the community (Smith and Tyler 1972; Helfman 1978). As body size increases, habitat selection will reflect the need to harvest resources while minimizing risk of predation. A number of studies of marine organisms have documented the differences in survival and growth among habitat and substrate types (Eckert 1985; Jones 1988) or have documented ontogenetic changes in habitat use (Helfman 1978; Robertson et al. 1979; Shulman 1985; Shulman and Ogden 1987; Jones 1988; Booth 1995). The costs and benefits of such habitat shifts have been measured by only a few researchers in aquatic systems. Using a series of elegant small-lake experiments, Werner and colleagues demonstrated that the timing of habitat shifts during ontogeny depends upon various trade-offs (Werner et al. 1983a, b, Werner and Gilliam 1984). For example, an individual that responds to differences in refuge characteristics and food resources may select a site which has better shelter but poorer food supply/quality and thus trade slower growth for increased survivorship. Conversely, more profitable habitats may

also be more dangerous due to poorer shelter characteristics or greater density of predators. The relative magnitude of these dynamic ecological relationships (growth vs. survival) will change with size, and with the foraging and escape ability of the individual (Werner and Hall 1988).

The response of individuals to spatial differences in resources may produce predictable spatial changes at the population level (Jones 1991). The densities of juvenile and adult coral reef fishes have been correlated to a variety of physical and biological characteristics of coral reef habitats including topographic complexity (Luckhurst and Luckhurst 1978; Thresher 1983; Roberts and Ormond 1987; Connell and Jones 1991; Sale 1991), Nemeth Chapter 2). Although a few studies have established relationships between different substrates and habitats and subsequent growth and survival of juveniles (Jones 1986,1988; Wellington 1992, Nemeth Chapter 1, 2), few have identified the critical resources or how postrecruitment processes affect subsequent population structure. In previous experiments (Chapter 1, 2, 3), I showed that rubble substrate offers *S. partitus* juveniles a recruitment microhabitat where growth and survival are elevated. The extent to which selection of rubble at settlement translates to greater population density remains unknown. However, limited evidence indicates that the spatial variability of critical juvenile habitats will determine not only the distribution patterns of different ontogenetic stages but may also affect the rate of increase of the adult population if these critical habitats are limited (Wahle and Steneck 1991).

In this study I examine the use of different substrates by naturally recruiting bicolor damselfish (*Stegastes partitus*) and the demographic changes that occur during ontogeny. Juvenile *S. partitus* typically recruit to mounds of small, slender coral rubble (*Porites porites, Acropora cervicornis*)

which accumulate at the edges of reefs or are constructed on sand flats by sand tile fish (*Malacanthus plumeri*). Adults and larger juveniles are predominately found on a variety of live coral species (*P. porites, Montastrea annularis*) and sponges. This distinct spatial distribution pattern is common throughout the Caribbean (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). In this paper I ask the following questions: Is rubble an important recruitment substrate which provides a distinct advantage to *S. partitus* juveniles over other common substrates? Does *S. partitus* shift from rubble to coral substrate during ontogeny? If so, is there a specific size at which this shift occurs? Finally, does this pattern of substrate use affect *S. partitus* population size? To address these questions I manipulated the amount of rubble substrate in large areas of the fore reef base and monitored subsequent settlement, mortality and migration of *S. partitus* juveniles over a 2.5 month period. By tagging resident adults and recruits, I was able to identify individuals 5 months later and assess the effect of movement and mortality on population growth.

MATERIALS AND METHODS

Photographic quadrats were used to determine if microhabitats used by bicolor damselfish were non-randomly distributed among available substrates and if they differed among juvenile (10-20 mm SL), intermediate (20-35 mm SL) and adult (>35 mm SL) size classes. A 30-m transect tape was laid parallel to the reef crest along the fore reef slope of Teague Bay, St. Croix at a depth of 8 to 15 m. When a bicolor damselfish was encountered within 1 m of each side of the tape, a 0.25 m^2 quadrat was centered within the territory occupied

by the damselfish and photographed. Although adults can defend territories up to 1 m^2 I was primarily interested in the center of their territories which is their primary site of refuge and reproduction (Schmale 1981). After all damselfish along the two meter strip were photographed, a random number table was used to determine the distance along the tape to photograph the "null" quadrats. Odd numbers designated the left side of the tape and even numbers the right.

Characterization of microhabitats was quantified by projecting the slide of each quadrat onto a grid of 100 dots, of which half (50) were randomly selected for analysis. The proportion of the 50 dots which fell on each substrate type determined its percent cover within that quadrat. Seven dominant substrate types were identified: 1) small rubble (< 2 cm diameter), 2) large rubble (> 2 cm), 3) *Porites porites*, 4) *Montastrea annularis*, 5) pavement and sand, 6) boulder and other corals (*Siderastrea* spp., *Diploria* spp., *Porites asteroides*, *Agaricia* spp., *Millepora* spp.), and 7) gorgonians, sea fans and sponges. These groupings were based upon similarities in their qualitative structural characteristics. A multivariate analysis of variance (MANOVA) compared the percent cover of the different substrate types (dependent variables) in the territories of three size classes of *S. partitus* and the null quadrats (independent variable).

To determine if the addition of rubble substrate increases settlement and subsequent population size, I established twelve 15 m x 15 m quadrats (225 m^2) along the fore reef base of Teague Bay (Fig. 1). Criteria for selecting large quadrats included the presence of isolated coral heads surrounded by barren sand. Steel reinforcement bars were driven into the sand at the corners of each quadrat. String was used to define the perimeter of each quadrat and to divide each large quadrat into 7.5 x 7.5 m quarters. Quadrats were randomly

assigned one of three treatments: no rubble (0 m^2), 5 m^2 of rubble, and 10 m^2 of rubble. In the 0 m^2 treatment quadrats all naturally occurring rubble piles were removed. In the 5 m^2 treatment quadrats, divers constructed 10 rubble piles (0.5 m^2) by either raking scattered rubble into piles, or collecting rubble from surrounding areas and moving it with lift bags. Rubble piles were placed equidistant between coral heads. The 10 m^2 treatment quadrats were treated similar to the 5 m^2 quadrats except that they contained twenty 0.5 m^2 piles of rubble spaced equally about the quadrat between the coral heads. Once quadrats were completed, photographs of quarter quadrats were taken to determine percent coral cover. Since the 2-dimensional nature of photographs underestimates the surface area of coral heads, I converted planar area to surface area of a hemisphere since most coral heads have this general shape. This allowed a direct comparison of percent area of the two substrates types. For each quadrat, I mapped the location of all coral heads and rubble piles onto waterproof graph paper. Templates of these maps were used to record the position of juvenile, intermediate and adult *S. partitus* (Fig. 2). All resident *S. partitus* were captured with nets and anesthetic (quinaldine) and tattooed underwater with 2 (intermediate) or 3 (adults) horizontal marks of red elastomer (Northwest Marine Technology, Inc.). Elastomer is an elastic liquid compound which, when mixed with a hardener and injected into a fish, hardens into an elastic tag. This tag has greater longevity than other dyes (pers. obs.) and does not cause reduction in growth as tattoo ink might (Forrester 1995). Juvenile recruitment, mortality and migration were recorded on 4 June, 2 July, 23 July, and 5 August. To differentiate fish which settled onto coral heads or rubble piles, I tattooed coral recruits with one blue line and rubble recruits with one orange line. Five months later (6-7 January 1996), I censused the 12 quadrats for tattooed

and non-tattooed juvenile, intermediate and adult *S. partitus*. Cumulative recruitment to 5 August 1995 and to 7 January 1996 were analyzed separately for differences among experimental rubble manipulations (0 m^2, 5 m^2 and 10 m^2 of rubble) with a one-factor ANOVA.

RESULTS

Percent cover of different substrates within *S. partitus* territories and within randomly chosen null quadrats was compared. Juveniles and adults selected territories with a greater percentage of small coral rubble and live *P. porites*, respectively, than would be expected at random (Table 1, Fig. 3). Moreover, percent cover of these two substrates was also significantly different between adult and juvenile size classes (Table 1). Since adults were more often found on live coral their territories contained less sand and pavement than was generally available in the surrounding habitat. Substrate composition within subadult territories was intermediate between adults and juveniles (Fig. 3).

Within the 12 large quadrats, juvenile *S. partitus* recruited to rubble at higher densities than to *M. annularis* coral (0.51 fish/m^2 vs. 0.07 fish/m^2, Table 2). Juveniles which settled to rubble represented 30% of the fish recruiting to about 6% of the available substrate. However, even though there was a positive trend between rubble density and total juvenile recruitment by the end of the summer (Fig. 4) this relationship was not significantly different among treatments ($F_{2,9}$=1.38, P=0.30). Of the four quadrats with 10 m^2 of rubble, quadrats #1, #7 and #10 received 11, 16 and 12 recruits, respectively, whereas quadrat #5 received only 3 recruits (Table 2).

The low number of recruits to quadrat #5 had strong leverage on the statistical outcome. If #5 was removed from the analysis the recruitment pattern became significant ($F_{2,8}$=7.303, P=0.016). After a 5 month period (August to January) the total juvenile recruitment, which includes surviving summer recruits plus fall recruits, was also greater in quadrats with more rubble but again this trend was not significant ($F_{2,9}$=0.917, P=0.434).

Table 1. Summary of multiple analysis of variance of microhabitat characteristics within adult (A = >35 mm SL), intermediate (I = 20-35 mm SL), and juvenile (J = <20 mm SL) territories, and within randomly selected null (N) sites on the fore reef slope of Teague Bay, St. Croix. Results of Tukey post-hoc test between age classes and null sites are shown for differences at P<0.05. ns = non-significant.

Substrate	SS	MS	$F_{(3, 105)}$	P	Tukey
Small Rubble	1571.6	523.9	4.13	0.008	J>A,N
error	13314.5	126.8			
Large Rubble	124.6	41.5	0.38	0.769	ns
error	11544.5	109.9			
Live *Porites*	629.9	210.0	4.41	0.006	A>J,N
error	5000.8	47.6			
Live *Montastrea*	267.0	89.0	0.85	0.469	ns
error	10970.0	104.5			
Pavement/Sand	889.2	296.4	2.85	0.041	N>A
error	10928.3	104.1			
Boulder coral	12.3	4.1	0.70	0.552	ns
error	613.9	5.8			
Soft Coral/Sponge	7.0	2.3	0.40	0.756	ns
error	614.5	5.8			

The decline in tattooed adults and juveniles between August and January was an estimate of mortality and emigration during that time period (Fig. 4). Average adult mortality over 5 months was about 65% with little migration of untagged adults into the quadrats to replace this loss.

Recruitment of juveniles in the fall nearly doubled the population of juvenile fish surviving from the summer but was still well below maximum summer levels. Of the 99 juveniles tattooed in August, 13 were seen again in January. During that five month period, 10% (7 of 70) of the recruits to coral and 21% (6 of 29) of the recruits to rubble had survived. This rate of mortality may have been influenced by two hurricanes (Louis and Marilyn) which passed over St. Croix in October 1995. However, a general survey of the fore reef area in January indicated that storm damage to the substrate was minimal in water deeper that 10 m. At shallower depths along the reef slope soft corals, sponges and macroalgae had been decimated. In the deeper areas, such as in my quadrats, no detectable disturbance was apparent. Surprisingly, not even the rubble piles showed evidence of excessive sedimentation or scattering.

Migration between different substrates occurred during the summer and fall. Larvae which settled to rubble shifted to the adult substrate at a size of 20 to 26 mm SL and as early as two weeks after settlement. The average distance moved by a migrating fish was 1.5 m. Eight of the 9 migrants (90%) moved toward or shifted onto coral heads occupied by conspecific adults. Over the 5 month period, juveniles which initially settled to rubble and then shifted to coral showed a 50% increase in survivorship over those fish settling directly to coral (21% vs. 10%, respectively). Since no juveniles remained on rubble by January, it is unknown whether these fish died after migration to coral or if they experienced greater mortality with age on rubble (see Discussion). Juveniles also shifted between coral heads. Twice during the summer, I documented a recruit, which had settled on a small coral head, set up a territory on an adjacent larger coral colony (Table 3).

Table 2. Summary data of 15 m x 15 m quadrats used in recruitment experiment on the fore reef base of Teague Bay. Rubble manipulation treatments were: 0 m^2, removal of all rubble; 5 m^2, addition of 10 0.5 m^2 piles of rubble; and 10 m^2, addition of 20 0.5 m^2 piles of rubble. Coral cover (primarily live *Montastrea annularis*) was measured using digitized photographs of quadrats. The planar area was converted to the surface area of a hemisphere which is a more accurate measure of surface area. Resident fish were first counted June 4 and recruit numbers (and density) were from last count on 5 August, 1995. Mortality estimates are based on tattooed fish which settled to rubble or coral and were resighted January 6, 1996.

Quadrat	Rubble Level (m^2)	Coral Cover (m^2)	Resident Fish at Start	Recruits to Rubble # (#/m^2)	Recruits to Coral # (#/m^2)	5 Month Survival rubble # (%)	5 Month Survival coral # (%)
2	0	86.6	23	-	7 (0.081)	-	2 (28.6)
4	0	88.2	16	-	4 (0.045)	-	0 (0)
8	0	64.7	6	-	5 (0.077)	-	0 (0)
11	0	82.8	24	-	10 (0.121)	-	0 (0)
total	0	322.3	69	-	26	-	2
average		80.6	17.2		6.5 (0.08)		0.5 (7.7)
3	5	97.4	13	6 (1.20)	3 (0.031)	0 (0)	0 (0)
6	5	83.4	17	3 (0.60)	3 (0.036)	0 (0)	0 (0)
9	5	72.9	23	2 (0.40)	8 (0.110)	2 (100)	0 (0)
12	5	69.4	6	1 (0.20)	5 (0.072)	0 (0)	1 (20.0)
total	20	323.1	59	12	19	2	1
average	5	80.8	14.8	3 (0.60)	4.8 (0.06)	0.5 (17)	0.25 (5.3)
1	10	67.9	13	7 (0.70)	4 (0.06)	1 (14.3)	0 (0)
5	10	111.7	6	1 (0.10)	2 (0.02)	1 (100)	0 (0)
7	10	73.9	10	5 (0.50)	11 (0.15)	1 (20.0)	1 (9.1)
10	10	69.1	23	4 (0.40)	8 (0.12)	1 (25.0)	3 (37.5)
total	40	322.6	52	17	25	4	4
average	10	80.6	13	4.2 (0.42)	6.2 (0.08)	1 (23.5)	1 (16)

Table 3. Documented cases of juvenile *S. partitus* which settled to rubble then shifted to coral within the 225 m^2 quadrats on the fore reef base of Teague Bay. † indicates fish which settled to coral then shifted to another coral head. See Table 1 for explanation of rubble manipulations. Fish lengths with a > symbol indicate the last measurement in August, 1995 before migration was detected in January, 1996.

Quadrat # (Rubble Area m^2)	Approx. Settlement Date (1995)	Migration Date	Length at Migration (mm SL)	Migration Distance (m)
1 (10)	May 31	7/2 - 7/21	26	2.4
2 (0)	July 2	†7/21 - 8/4	23	1.6
5 (10)	July 31	8/4 - 1/6	>20	2.0
6 (5)	July 10	7/10 - 7/22	20	0.5
7 (10)	July 13	8/5 - 1/6	>23	1.5
9 (5)	July 1	8/10 - 1/7	>25	1.5
9 (5)	July 23	8/5 - 1/7	>20	1.5
10 (10)	July 1	†7/10 - 7/23	20.5	1.1
10 (10)	July 1	7/1 - 7/17	20	1.0

DISCUSSION

Analysis of microhabitat characteristics of juvenile, intermediate and adult territories confirmed the distinct ontogenetic distribution patterns of bicolor damselfish (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Percent cover of small rubble in juvenile territories and live *Porites* coral in adult territories was significantly different from a random sample of available substrates. Moreover, the significant differences between substrate use of juveniles and adults provided evidence that larvae select small rubble at settlement then shift to other substrates with age. This pattern was supported by the lack of a significant difference in substrate use between subadults and the larger and smaller size classes. Intermediate sized fish were in transition between juvenile and adult substrates.

By manipulating the amount of small rubble within 225 m^2 quadrats and by monitoring subsequent settlement and recruitment within these quadrats, I was able to document the demographic "response" of individual recruits to this substrate and the relative importance of this "response" to the local population. Within the 12 quadrats, rubble made up 6% of the available substrate but received about 30% of the recruits. However, juveniles which settled onto rubble readily shifted to *M. annularis* coral as early as 2 wk postsettlement at a size of 20 to 26 mm SL.

This pattern of substrate use has important demographic consequences for the individual and the local population. After 5 months, juveniles which initially settled to rubble and then shifted to coral showed a 50% increase in survivorship over fish settling directly to coral (21% vs. 10%, respectively). The importance of recruitment habitats is known for a variety of organisms in a diversity of environments (Werner et al. 1983; Herrnkind and Butler 1986; Schlosser 1987; Werner and Hall 1988; Wahle and Steneck 1991; Eggleston and Lipcius 1992; Sweitzer and Berger 1992). The choice of recruitment habitat is closely associated with juvenile body size, foraging efficiency and intensity of predation. In Chapters 2 and 3, I showed that *Porites* rubble provided greater refuge from predation due to its shelter characteristics and that juveniles grew at faster rates in rubble relative to *Montastrea* coral. Thus juvenile *S. partitus* gain multiple benefits by recruiting to rubble substrate. These findings contrast those of Werner and Hall (1988) who found that habitat shifts in the bluegill sunfish (*Lepomis macrochirus*) are related to a growth rate-predation risk trade-off. Juvenile *L. macrochirus* take refuge from predation by largemouth bass (*Micropterus salmoides*)in the food-limited vegetated littoral zone at a size of 12.5 mm to 50 to 83 mm SL. The shift back to the more profitable pelagic habitat occurs

when the risk of predation decreases with increasing juvenile size (Werner and Hall 1988).

The shift from rubble to coral by juvenile *S. partitus* is probably a function of the benefits of increased growth and survival in rubble and the increasing drive for reproduction at maturity. As a juvenile grows, the abundance of small shelters provided by rubble substrate (Chap. 2) will become less accessible. Sedimentation of rubble substrate further reduces the quality of this refuge for larger fish. Thus the initial advantage gained early in life slowly decreases with increasing size. As *S. partitus* approaches maturity, those fish which shift to substrates with better nest sites will increase their reproductive fitness (Itzkowitz 1985, 1991). Sadovy (1986) found that sexual differentiation in *S. partitus* occurs between 20 to 25 mm SL which corresponds well with the size at which relocation to *Montastrea* coral occurred (20 - 26 mm SL). At maturity (30-35 mm SL) reproductive fitness will increase the sooner a fish has access to other reproductively mature conspecifics. Ninety percent of the fish which shifted from rubble to coral or from coral to coral moved onto or toward coral heads occupied by conspecific adults. This behavior created a clumped distribution pattern reported by Sadovy (1986). The existing tradeoff between shifting sooner to secure a superior territory in the adult habitat and being more vulnerable to predators has not been reported previously for marine fishes.

Models for predicting the optimum size for ontogenetic shifts have been proposed to explain a range of ecological patterns from the distribution of different age classes (Werner and Hall 1988) to predicting the optimum size at which sex change should occur in hermaphroditic fishes (Ghiselin 1969; Warner 1988). The optimum time to shift from one substrate to another can be modeled for juvenile *S. partitus* (Fig. 5). In the model, larvae (10-15 mm)

which settle onto rubble gain immediate benefits in terms of survival and growth over fish which settle onto coral. As these fish increase in size, the relative benefits decrease since fish which survive on coral become less vulnerable to predation as they grow. Moreover, as juveniles approach maturity, fish which are already living on coral will have priority access to vacancies in spawning habitat due to mortality of resident adults (Sale et al. 1980). Fish which remain on rubble will experience increased risk of predation because the abundance of small shelters provided by rubble substrate will become less accessible to larger fish. The vulnerability of adults on rubble piles was observed numerous times. When rubble piles were first constructed they were occasionally colonized by neighboring adults because the new rubble piles provided some large shelters and even suitable nesting sites which were easily defended and lacked the invertebrate egg predators of more established territories (Itzkowitz 1985; Knapp and Kovach 1991). However, when approached by a diver, the adult fish would often retreat to the *Montastrea* coral head from which it came. Juveniles which recruited to rubble piles never left this refuge. After several weeks, rubble piles would begin to settle and interstices fill with sediment reducing its suitability to adult fish. The steep drop in overall fitness of large fish living on rubble is indicated in the model (Fig. 5). The optimum strategy of juvenile bicolor damselfish would be to settle to rubble substrate then shift to coral at the opportune time. Timing of movement (intersecting lines) would depend upon a fish's perceived risk of predation which would be a function of its size, the density of predators, and the distance to other substrates. Presence of predators and perceived risk of predation by prey has been shown to alter movement patterns of even strongly migratory species (Helfman 1986).

Models, such as described above, may also be used to predict the population response to changes in primary recruitment habitats or substrates. If primary juvenile habitats are limited, adult populations of short lived species may also be limited even if adult habitats are not saturated. The life span of *S. partitus* is about two years with the average adult being one year old (Schmale 1981; Robertson 1996). Increasing the amount of recruitment habitat should have positive effects at the population level. However, if an area is dominated by substrate suitable only for juveniles, the adult habitat may become the limiting resource. Although the patterns of increasing population size in quadrats with more rubble (primary recruitment substrate) were inconclusive, the trend was in the predicted direction (Fig. 4). The experiment was probably too short in duration to show substantial changes in the adult population. Several studies examining the response of coral reef fish populations to experimental manipulations did not detect population changes until several years later (Jones 1987; Schmitt and Holbrook 1990; Robertson 1996). Robertson (1996) found that when released from interspecific competition, *S. partitus* population densities started to increase within a year but only reached their maximum in about 4 years. The results of my study suggest that enhancement of recruitment habitats, even at a small scale, may influence population structure if followed over several generations. The use of specific habitats by juveniles and the associated benefits of enhanced growth and survival suggests that species-specific patterns of habitat use are a means of maximizing overall fitness. Establishing the relative importance of fish-habitat associations and their affects on population dynamics will reveal some of the important ecological processes which structure reef fish communities.

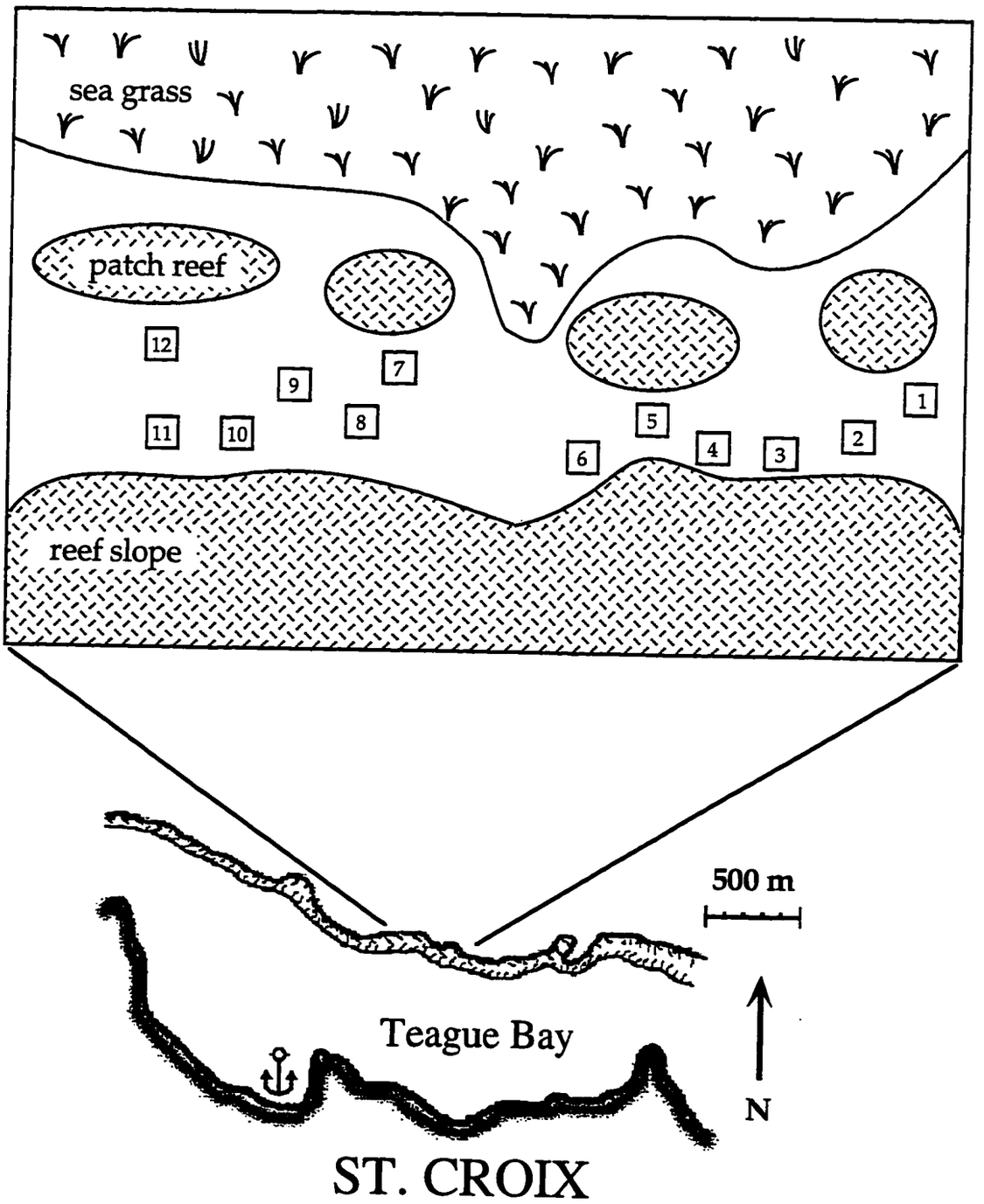

Figure 1. Approximate locations of the twelve 15 m x 15 m quadrats along the fore reef base of Teague Bay, St. Croix. Quadrats were located on the reef base between the fore reef slope and manatee grass beds (*Syringodium filiforme*). This area consisted of isolated coral heads and rubble surrounded by bare sand. Anchor indicates location of St. Croix Yacht Club.

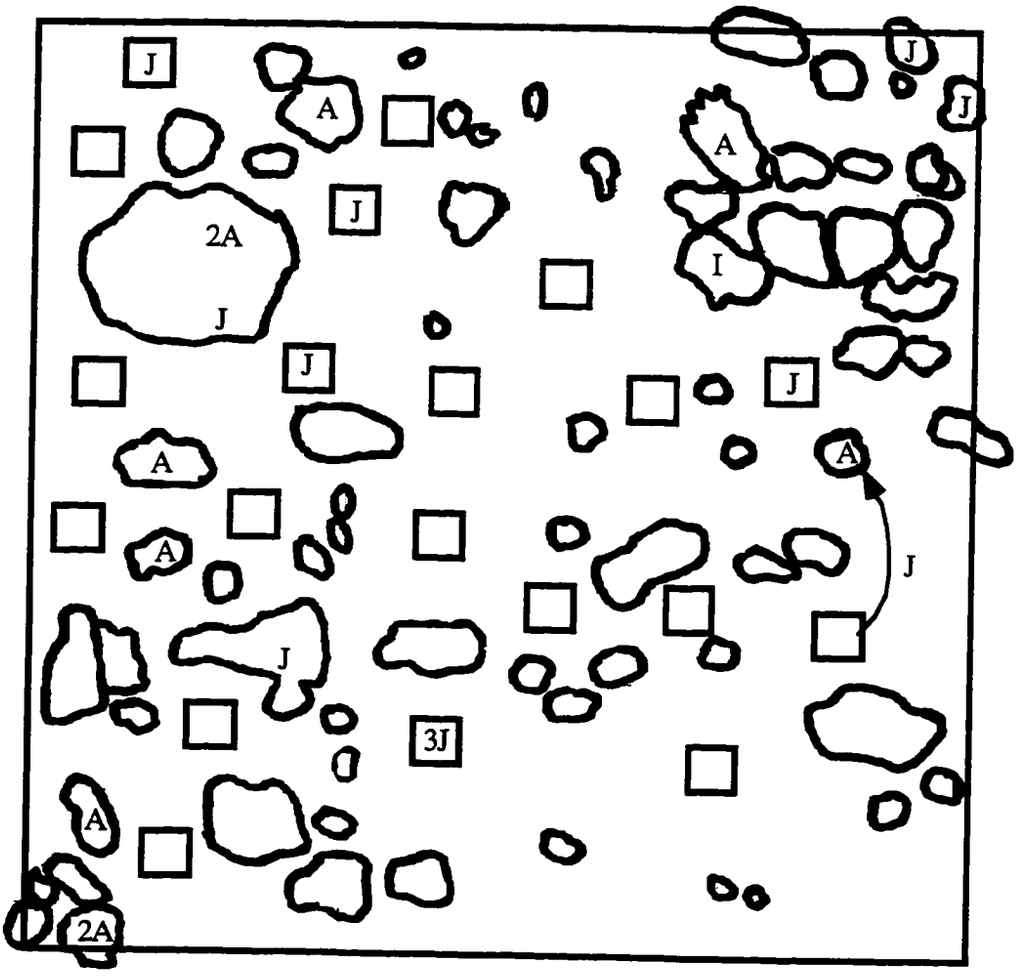

Figure 2. Map of Quadrat 1 on 4 August, 1995 showing location of juvenile recruits (J), resident adults (A, >35 mm SL) and intermediate (I, 20 to 35 mm SL) *S. partitus*, on coral and rubble substrate. Irregular shaped objects indicate *Montastrea annularis* coral heads and squares are rubble piles. Numbers preceding letters indicate number of fish at that location. Arrow on right shows the migration direction of a juvenile from rubble to coral 2.4 m away.

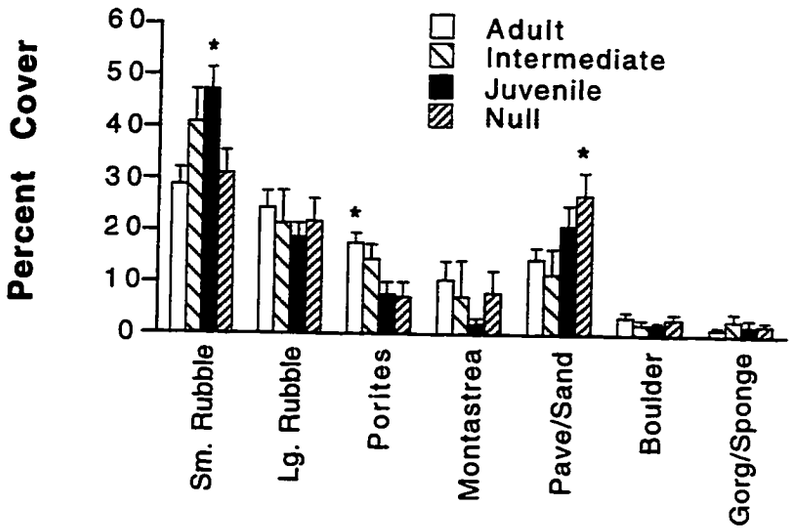

Figure 3. Percent cover (+ standard error) of dominant substrates within randomly selected 'null' sites and within adult (>35 mm SL), intermediate (20-35 mm SL), and juvenile (10-20 mm SL) *S. partitus* territories on the fore reef slope of Teague Bay, St. Croix. Substrate categories include small rubble (<2 cm diameter), large rubble (>2 cm), live *Porites porites*, live *Montastrea annularis*, pavement (pave) and sand, boulder corals (*Siderastrea* spp., *M. cavernosa*, *Diploria* spp.), gorgonians and sea fans (soft), and sponges. *P<0.05. See Table 1 for pairwise comparisons.

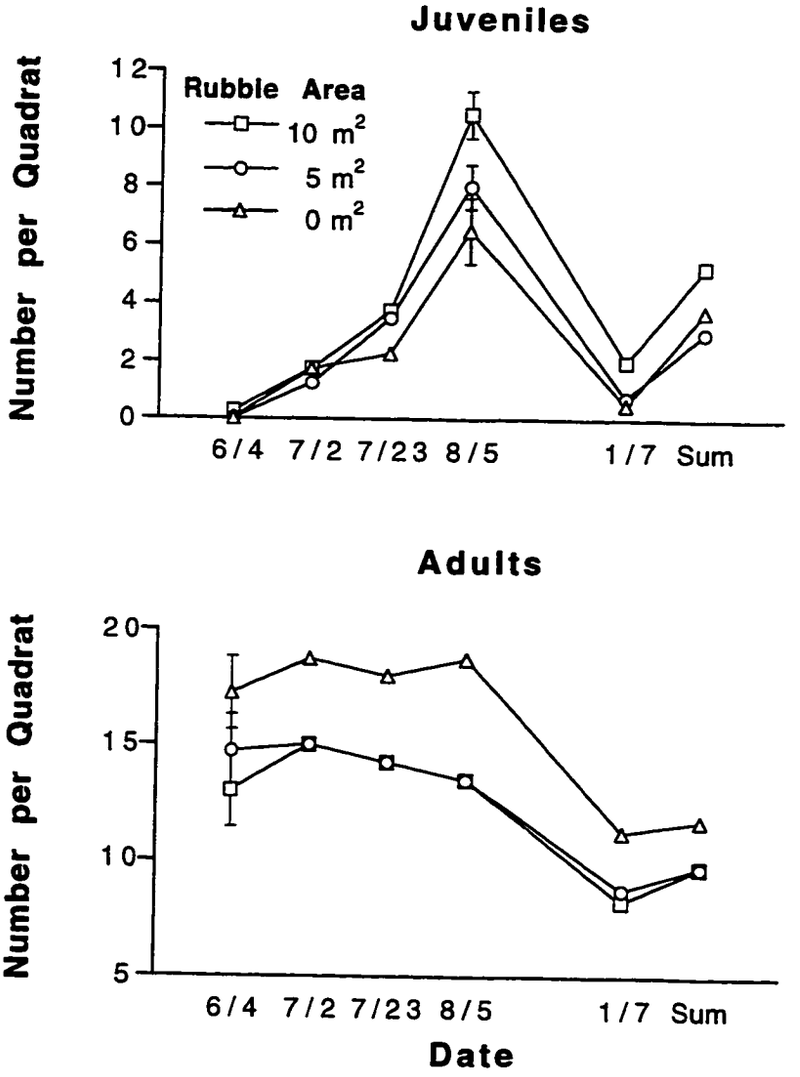

Figure 4. Results of rubble manipulation experiment showing number of Juvenile and Adult (adult + intermediate) *S. partitus* counted in June (6/4), July (7/2, 7/23) and August (8/5), 1995 and January (1/7), 1996. January 7 date shows only fish which had tattoos from summer tagging and thus is an estimate of survival over 5 months. Sum includes all tattooed fish plus fish without tattoos (recruitment and migration since August 5, 1995). Error bars are mean square errors pooled within each treatment.

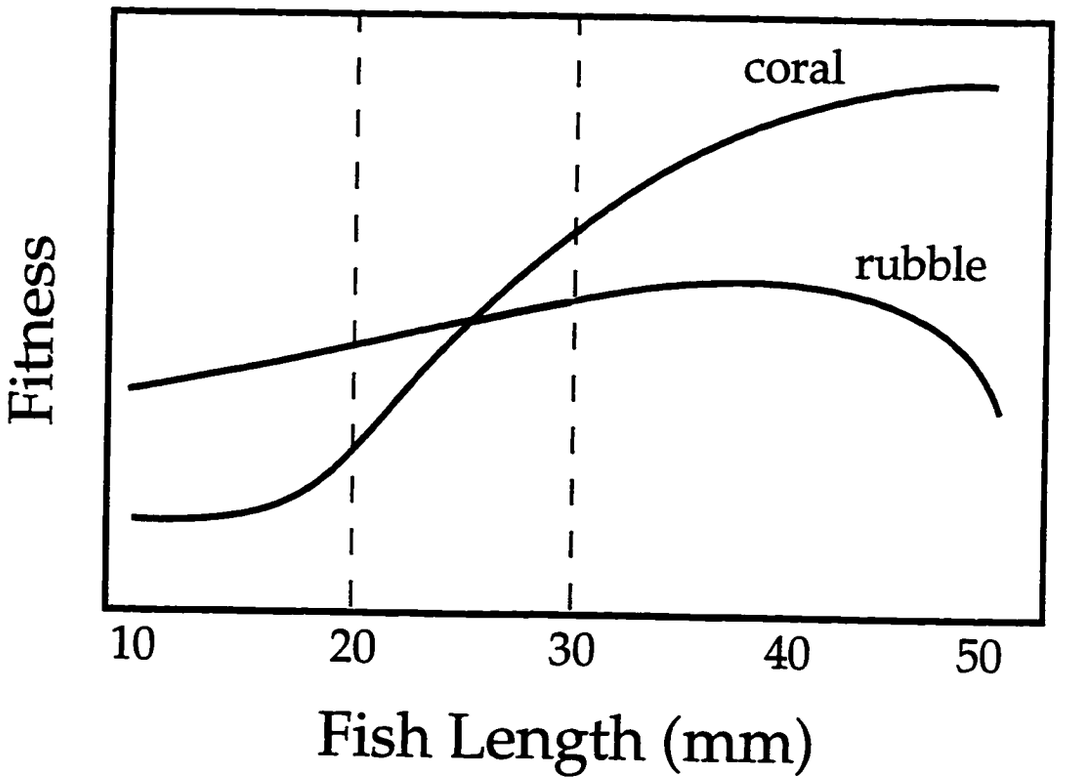

Figure 5. Model of the optimum size at which to shift substrates. Greatest overall fitness will be achieved if juvenile *S. partitus* settle onto small rubble substrate then shift to coral substrate (includes *M. annularis, P. porites,* large rubble or sponges) when lines cross. The dashed line at 20 mm indicates the onset of sexual maturity (gonad formation) and the smallest fish I observed to switch. Dashed line at 30 mm indicates smallest size of reproductively active *S. partitus* (Sadovy 1986). The optimum size to shift substrates (location of line intersection) will depend upon vacancy in surrounding habitats, distance to nearest adult substrate and predation risk. If switch is delayed too long, fitness of individual will drop dramatically because as it grows small rubble will become less suitable as a refuge from predation.

CHAPTER V

ECOLOGICAL PATTERNS DURING ONTOGENY: A SYNTHESIS

Coral reef fishes have open populations connected at the meta-population level through dispersive larvae (Roughgarden et al. 1988; Sale 1991). The planktonic larval phase, the transition to the benthic juvenile form and the period preceding maturity each impose a unique set of constraints during the lifetime of the individual. The magnitude of these constraints will be age-dependent and species-specific and will thus influence species distribution and abundance patterns during ontogeny. Integrating these components of complex life histories is necessary to fully understand the importance of each stage and was the focus of this dissertation.

The exportation of eggs and larvae from the adult habitat marks the beginning of the pelagic stage where larvae experience a broad range of environmental conditions which influence growth and time spent in the plankton (Thorson 1950; Thorrold et al. 1994). Marine biologists have suggested that adults of both tropical (Johannes 1978; Doherty 1983; Lobel and Robinson 1986; Lobel 1989; Robertson et al. 1990) and temperate (Smith et al. 1978, Colton et al. 1979, Neilson et al. 1988) fishes have predictable spawning locations and behaviors which may reduce risk of egg or larval predation or increase entrainment into favorable currents for enhancement of larval growth and survival. Using otoliths as my primary tool to investigate larval

history of the bicolor damselfish (*Stegastes partitus*), I discovered that variability in growth during the pelagic phase was extremely important in determining planktonic duration (Chap. I). Individuals which had elevated growth rates during the first week post-hatching reduced the time required to reach competency and were younger and smaller at settlement. This is the first evidence providing an explanation for variation in larval duration, a phenomenon which has perplexed marine scientists for decades (Victor 1991). Variability in larval duration was generally correlated to reproductive strategy. Pelagic-spawning species which broadcast their eggs (e.g. Labridae) have larvae with longer and more variable planktonic durations while demersal-spawning species (e.g. Pomacentridae) have larvae with shorter and less variable planktonic durations (Victor 1986; Wellington and Victor 1989; Thresher 1991). For broadcast-spawning species, whose larvae tend to disperse farther offshore (Leis 1983), the ability to delay metamorphosis and the resultant flexibility in the timing of settlement may be an adaptation for maximizing the return of larvae to coastal waters (Jackson and Strathmann 1981; Victor 1986). Therefore, variation in plankontic duration of pelagic spawners will depend upon the presence of a settlement cue at competency. Alternatively, variation in settlement age of demersal-spawning species, whose larvae are often within 1 km of shore (Leis 1991), is causally linked to variation in growth rates early in life. Elevated growth rates for some individuals may reflect differences in synchronization of morphological development (Liem 1991), larval feeding behavior (Blaxter 1986), environmental variability (Kingsford 1990) or a combination of these factors.

In order to integrate life history transitions we need to determine the relative magnitude of different processes occurring in early life history stages and their effects on later stages. Based on the findings of other studies

(Labelle and Nursall 1985; Cowen 1991; McCormick and Molony 1992), I expected that larvae with different presettlement histories would have varying abilities to successfully make the transition to the benthic environment. However, in my study size and age at settlement had no effect on post-settlement survival whereas elevated growth near the end of larval phase seemed to span metamorphosis and continue in the settled individual. The lack of effects of size and age are consistent with the results of Bertram and Leggett (1994) for winter flounder (*Pleuronectes americanus*). However, the positive correlation between larval and juvenile growth rates of wild caught *S. partitus* does not match patterns of growth of laboratory reared *P. americanus* (Bertram et al. 1993). They found that within 1 to 7 weeks after metamorphosis, compensatory growth of slower growing larvae converged the size and age of juveniles from different cohorts. It is possible that if I had measured growth beyond the first 10 days post-settlement, I may have achieved similar results.

Despite the potentially significant influence of larval growth on post-settlement events (Rowe and Ludwig 1991), I found that the consequences of larval settlement behavior had a substantially greater effect on post-settlement survival and growth than did larval history. The small-scale (10's of meters) distribution of larvae among two substrate types was largely determined by active selection of small rubble substrate (Chap. I). These patterns were enhanced by differential mortality most likely due to the structural architecture of the substrate (Chap. I, II). These results corroborate numerous studies documenting the differential effects of microhabitat characteristics on juvenile fishes and invertebrates (Sale et al. 1984; Herrnkind and Butler 1986; Clarke 1989; Breitburg 1991; Levin 1991; Tolimieri 1995). However, I found that the increased growth and survival experienced

by *S. partitus* on rubble substrate only benefits small juvenile fish. As fish size increases and maturity approaches, other substrates (e.g. *Montastrea annularis*) will be more suitable for shelter and reproduction and should favor those fish shifting to more appropriate substrates. Larval *S. partitus* which initially settled onto small rubble and then shifted to coral had a 50% increase in survivorship over those larvae which settled directly to *M. annularis* coral (Chap. IV). The costs and benefits of such habitat shifts in fishes have been measured by only a few researchers in freshwater lakes (Werner et al. 1983; Werner et al. 1983; Werner and Gilliam 1984). Although a number of studies have documented habitat shift in marine systems (Helfman 1978; Robertson et al. 1979; Shulman 1985; Shulman and Ogden 1987; Jones 1988; Booth 1995) this is the first to document the benefits of such a shift and a graphical model was developed which predicted the timing of habitat shifts during ontogeny.

At larger spatial scales (100's of meters), variation in biotic and abiotic factors among reef zones (back reef vs. fore reef) strongly influenced juvenile *S. partitus* demography and subsequent population abundance (Chap. I, III). Previous studies examining the structure of reef fish populations have contrasted the importance of variation in the arrival of colonizing individuals (review by Doherty and Williams 1988, Doherty and Fowler 1994) with the effects of processes occurring after settlement such as competition (Smith and Tyler 1972; Ehrlich 1975; Gladfelter et al. 1980; Forrester 1995; Robertson 1996) and predation (Talbot et al. 1978; Shulman 1985; Shulman and Ogden 1987; Hixon 1991). The view that a single mechanism is responsible for population regulation is over-simplified (Richards and Lindeman 1987; Warner and Hughes 1988), especially when one considers the great spatial heterogeneity of coral reefs over a wide range of scales.

The relative magnitude of different factors on population structure is illustrated using results from a multifactorial study conducted at various spatial scales (Chap. III). For example, larval *S. partitus* that settle to the fore reef on *Porites* rubble without interspecific competitors become mature in about 6 months (Fig. 1). Combining these measures of growth with mortality rates under the same conditions, about 35% to 40% of a cohort survive to reach reproductive maturity (Fig. 1). Alternatively, larval *S. partitus* settling to the back reef on *Montastrea* coral with *S. leucostictus* take twice as long to reach maturity. However, since mortality rates under these conditions are greater, few, if any, juveniles survive to adulthood (Fig. 1).

Under natural conditions the density of territorial competitors (*S. leucostictus* and *S. planifrons*) is substantially greater and the supply of planktonic organisms is substantially reduced on back reef habitats. The relative magnitude of the effects of benthic factors are greater than the effects of larval supply in structuring the population of *S. partitus* in back reef habitats of St. Croix. On fore reef habitats these negative factors are alleviated causing an increase in juvenile growth and survival relative to back reef habitats. Decreasing the effect of these benthic factors increases the relative importance of larval supply in affecting adult numbers on fore reef habitats. When I compared these parameters at an even larger scale (1000's of km), among the islands of St. Croix and Jamaica, the demographic responses of *S. partitus* juveniles were very similar. One prominent difference in Jamaica, however, was the greater influence of predation on juvenile survival (Chap. III).

These results illustrate the need to conduct experimental studies at various spatial scales and on a range of potentially important factors. Generalizations from results conducted at single locations can result in

extremely different conclusions. For example, a study conducted on the back reef of Teague Bay, St. Croix would conclude that interspecific competition would be very important in structuring *S. partitus* populations. A similar experiment on the fore reef would conclude that recruitment was regulating population size. On the fore reef in Jamaica, the effects of predation would dominate the experimental outcome. Studies which report growth and mortality without distinguishing among substrate types, reef habitats or the density of competitors or predators fail to account for potentially important factors (see McGehee 1995) and make comparisons of demographic rates between locations nearly impossible.

Obviously the problem of studying the interactions of fish and their environment lies in the large range of spatial scales over which different processes may affect population patterns. Previous studies examining the factors affecting reef fish populations have provided a wealth of detailed information on differences among species. Unfortunately this approach does not allow generalizations to emerge for inter- and intraspecific comparisons of population processes at various spatial scales. Spatial similarities in a species' population structure between different habitats and among comparable but distant habitats provide the best opportunity to test the ecological processes that may be responsible for the patterns observed. By using this approach I was able to account for the patterns of distribution and population structure of *S. partitus* found among different substrates and reef habitats throughout its geographic range (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Whether such biological and physical factors interact to influence the distribution and population structure of other reef fishes will need to be tested. It is likely, though, that the relative magnitude of such effects are more pronounced on strongly site-attached

species such as pomacentrids. More mobile species, which can use schooling as a predator defense mechanism (Pitcher 1986), will most likely migrate greater distances to those habitats that best fulfill their needs during ontogeny.

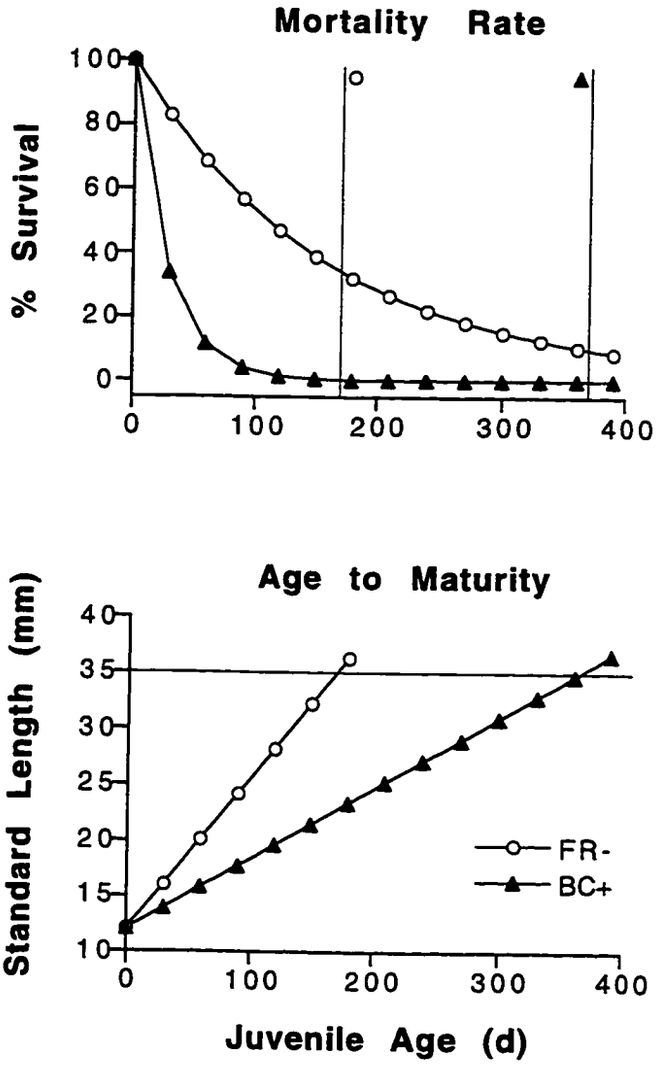

Figure 1. Projected time for newly settled *S. partitus* fish to reach maturity (horizontal line at 35 mm SL) based on growth rates for fish settling in the fore reef on *Porites* rubble without interspecific competitors (FR-) and fish settling in the back reef on *Montastrea* coral with interspecific competitors present (BC+). Percent of a cohort to reach maturity (vertical lines) based on survival rates for fish settling to conditions described above. Growth and survival curves represent the maximum and minimum bounds experienced by juvenile *S. partitus* fish. All other combinations of benthic processes examined would fall between these extremes with the exception of the effects of site-specific predation intensity on survivorship.

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